EVOLUTIONARY BIOLOGY OF SIPHONOSTOMATOIDEA (COPEPODA)
PARASITIC ON VERTEBRATES

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming
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THE UNIVERSITY OF BRITISH COLUMBIA
July 1993
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Abstract

A phylogeny for the 18 families of Siphonostomatoida (Copepoda) parasitic on vertebrates is presented which considers these taxa a monophyletic group evolved from siphonostome associates of invertebrates. Discussion of the evolutionary biology of these families is presented using this phylogeny as a foundation for comparison.

Siphonostomes typically attach at specific locations on their hosts. Although copepod morphology can sometimes be used to explain realized niches, most copepod distributions remain mysteriously confined. Distribution data suggest that the branchial chambers were the first regions of the vertebrate body to be colonized, and that the olfactory capsules of vertebrates may have been derived from some premandibular branchial component which caused an evolutionary split in the copepod fauna infecting the branchial chambers of noseless and jawless vertebrates. The general body surfaces of vertebrates were probably colonized by taxa infecting the gills and olfactory capsules, and perhaps was facilitated by a new type larva possessing a frontal filament. Adults of these larvae appear to have developed two modes of extending this progress in attachment security throughout adulthood. One mode involved new methods of permanent attachment of mature females, while the second mode allowed both powerful swimming and efficient suckorial attachment.

Reduction in the number of molts required to reach adulthood is exhibited by some lineages, and seems to have been realized through amalgamation of free living nauplius and/or parasitic copepodid stages. The first copepodid serves as the initial infective stage throughout all lineages.

While most siphonostome taxa are monoxenous, at least some pennellids are heteroxenous. Evolution of two host life cycles perhaps was facilitated by a highly mobile young adult capable of infecting another host, and by the close ecological association of the intermediate and definitive hosts.

Although not widespread, mesoparasitism has apparently evolved several times among siphonostome taxa infecting vertebrates. Phylogenetic data illustrate that once a lineage becomes mesoparasitic, reversal to ectoparasitism is uncommon.

Two siphonostome lineages have successfully invaded fresh water. This significant ecological shift appears to have been facilitated by a number of morphological, developmental, and ecological traits.

Preliminary studies suggest that siphonostomes have sometimes coevolved with their vertebrate hosts while at other times they have colonized phylogenetically distant but ecologically similar hosts. Overall, the speciation rate of these copepods seems to have lagged behind that of potential host taxa.
Table of Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>ii</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>iii</td>
</tr>
<tr>
<td>List of Tables</td>
<td>vi</td>
</tr>
<tr>
<td>List of Figures</td>
<td>vii</td>
</tr>
<tr>
<td>Acknowledgements</td>
<td>ix</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>2</td>
</tr>
<tr>
<td>BIOLOGY OF SIPHONOSTOME FAMILIES PARASITIC ON VERTEBRATES</td>
<td>5</td>
</tr>
<tr>
<td>Eudactylinidae Biology</td>
<td>5</td>
</tr>
<tr>
<td>Kroyeriidae Biology</td>
<td>8</td>
</tr>
<tr>
<td>Hatschekiidae Biology</td>
<td>11</td>
</tr>
<tr>
<td>Pseudocycnidae Biology</td>
<td>12</td>
</tr>
<tr>
<td>Hyponeoidae Biology</td>
<td>13</td>
</tr>
<tr>
<td>Lernanthropidae Biology</td>
<td>14</td>
</tr>
<tr>
<td>Dichelesthiiidae Biology</td>
<td>16</td>
</tr>
<tr>
<td>Pennellidae Biology</td>
<td>18</td>
</tr>
<tr>
<td>Sphyriidae Biology</td>
<td>23</td>
</tr>
</tbody>
</table>
**Section** | **Page**
--- | ---
Lernaeopodidae Biology | 25
Naobranchiidae Biology | 30
Tanypleuridae Biology | 30
Dissonidae Biology | 31
Pandaridae Biology | 32
Cecropidae Biology | 37
Trebiidae Biology | 38
Euryphoridae Biology | 39
Caligidae Biology | 40

**SIPHONOSTOME RELATIONSHIPS** | 43
Monophyletic Siphonostomatoida | 44
Monophyly of Siphonostomes Parasitic on Vertebrates | 45
Interfamilial Relationships Among Siphonostomes Parasitic on Vertebrates | 48

**EVOLUTIONARY BIOLOGY OF SIPHONOSTOMES PARASITIC ON VERTEBRATES** | 63
Trends in Larval Development | 64
Trends in Adult Natural History | 69
Trends in Host Associations | 76
Invasion of Fresh Water | 80
Temporal Origin of Siphonostomes Parasitic on Vertebrates | 87

**SUMMARY AND CONCLUSIONS** | 90
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>REFERENCES</td>
<td>94</td>
</tr>
<tr>
<td>TABLES</td>
<td>108</td>
</tr>
<tr>
<td>FIGURES</td>
<td>111</td>
</tr>
<tr>
<td>APPENDIX</td>
<td>168</td>
</tr>
</tbody>
</table>
List of Tables

*Table*  

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 1 Apomorphy list supporting Figure 21</td>
<td>109</td>
</tr>
<tr>
<td>Table 2 Numbers of copepod species infecting various body regions of some sharks in the western North Atlantic</td>
<td>110</td>
</tr>
</tbody>
</table>
List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>112</td>
</tr>
<tr>
<td>2</td>
<td>114</td>
</tr>
<tr>
<td>3</td>
<td>116</td>
</tr>
<tr>
<td>4</td>
<td>118</td>
</tr>
<tr>
<td>5</td>
<td>120</td>
</tr>
<tr>
<td>6</td>
<td>122</td>
</tr>
<tr>
<td>7</td>
<td>124</td>
</tr>
<tr>
<td>8</td>
<td>126</td>
</tr>
<tr>
<td>9</td>
<td>128</td>
</tr>
<tr>
<td>10</td>
<td>130</td>
</tr>
<tr>
<td>11</td>
<td>132</td>
</tr>
<tr>
<td>12</td>
<td>134</td>
</tr>
<tr>
<td>13</td>
<td>136</td>
</tr>
<tr>
<td>14</td>
<td>138</td>
</tr>
<tr>
<td>15</td>
<td>140</td>
</tr>
<tr>
<td>16</td>
<td>142</td>
</tr>
<tr>
<td>17</td>
<td>144</td>
</tr>
<tr>
<td>18</td>
<td>146</td>
</tr>
<tr>
<td>19</td>
<td>148</td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
</tr>
<tr>
<td>------------------------</td>
<td>------</td>
</tr>
<tr>
<td>20 Large gathering of female <em>Caligus productus</em> on roof of yellowfin tuna buccal cavity</td>
<td>150</td>
</tr>
<tr>
<td>21 Hypotheses of phylogenetic relationships of siphonostome families parasitic on vertebrates</td>
<td>152</td>
</tr>
<tr>
<td>22 Mouth tubes of two elasmobranch infecting pandarids</td>
<td>154</td>
</tr>
<tr>
<td>23 Frontal glands on ventral surface of two adult female pandarids</td>
<td>156</td>
</tr>
<tr>
<td>24 Sternal elements of two caligiform copepods</td>
<td>158</td>
</tr>
<tr>
<td>25 <em>Phyllothyreus cornutus</em> female maxilliped</td>
<td>160</td>
</tr>
<tr>
<td>26 Life cycle summaries for siphonostomes parasitic on vertebrates</td>
<td>162</td>
</tr>
<tr>
<td>27 Ecological summary cladogram of siphonostomes parasitic on vertebrates</td>
<td>164</td>
</tr>
<tr>
<td>28 Comparison of the gills and olfactory sacs of elasmobranchs</td>
<td>166</td>
</tr>
</tbody>
</table>
Acknowledgements

So many people made this work possible that it is difficult to single out individuals for acknowledgement. However, special salutes are due M. L. Adamson (The University of British Columbia), G. A. Boxshall (British Museum of Natural History), D. R. Brooks (The University of Toronto), J. N. Caira (The University of Connecticut), F. G. Carey (Woods Hole Oceanographic Institute), J. G. Casey (The National Marine Fisheries Service), R. F. Cressey (United States National Museum), G. B. Deets (The University of British Columbia), J-S. Ho (The University of California at Long Beach), W. E. Hogans (Atlantic Reference Centre, N.B.), K. Izawa (Mie University), Z. Kabata (formerly of The Pacific Biological Station), N. Kohler (The National Marine Fisheries Service), P. R. Last (CSIRO, Division of Fisheries), A. G. Lewis (The University of British Columbia), H. W. Pratt, Jr. (The National Marine Fisheries Service), G. G. E. Scudder (The University of British Columbia), G. B. Skomal (Massachusetts Division of Marine Fisheries), and C. E. Stillwell (formerly of The National Marine Fisheries Service) for having so generously provided that which the author lacked. This study was partially supported by University of British Columbia Graduate Fellowships and Teaching Assistantships to the author, as well as by operating grants from The Natural Sciences and Engineering Research Council of Canada to M. L. Adamson (The University of British Columbia) and D. R. Brooks (formerly of The University of British Columbia).
INTRODUCTION

Subclass Copepoda is composed of ten orders, together containing more than 10,000 described species (Huys and Boxshall, 1991). Over 2000 copepod species are considered parasitic (Cressey, 1983); however, as differences among commensal, mutualistic, and parasitic lifestyles are not often apparent without close inspection, the exact symbiotic status of many copepod associations is unknown. Siphonostomatoida Thorell, 1859 contains over 1550 species, of which some 1050 are generally regarded as parasites of vertebrates (almost exclusively fishes), about 500 are regarded as associates of invertebrates, and several species have no known host affiliation (Huys and Boxshall, 1991). Siphonostomatoida is basically a marine lineage, well-represented from abyss to surf, with only two families (both parasites of fishes) containing freshwater representatives (see Kabata, 1979).

Approximately 75 percent of all copepod parasites of fishes are siphonostomes (Yamaguti, 1963; Kabata, 1982), and 18 of 40 siphonostome families are composed of species that can be considered exclusive parasites of fishes. Taken together, these 18 families represent the most successful crustacean group parasitic on vertebrates, and as a whole they exhibit an interesting diversity of morphological, ecological, and developmental traits. Morphologically within these families taxa range from those easily recognized as siphonostomes to others which have defied classification as crustaceans. Ecologically differences regarding the preference to infect particular hosts and infection sites on the host are evident. Even more noticeable are the facts that although most species are marine inhabitants some species are true freshwater residents, and that although most species are ectoparasitic (i.e. they attach to the host in a superficial manner) some species are mesoparasitic (i.e. they attach by significantly penetrating the host while still leaving a portion of their body in full contact with the external environment). Also notable is that
while most taxa possess a one host life cycle, one family is well-known to contain species
with a two host life cycle. Developmentally, differences in life cycles both within and
among siphonostome families parasitic on vertebrates exist, with these differences
concerning the total number of life history stages, the number of stages which are capable of
infecting the host, and the morphology of developmentally equivalent life history stages.

The rich biological diversity displayed by the siphonostomes parasitic on vertebrates raises
some obvious evolutionary questions. Specifically, can primitive states and general
evolutionary trends be identified from the mixture of morphological, ecological and
developmental traits exhibited by these parasites, and how might such states and trends be
related to this group's success?

This thesis addresses the evolutionary biology of siphonostomes that infect vertebrates. In
doing so it attempts to interpret the biological significance of the morphological, ecological,
and developmental diversity exhibited by these copepods with respect to an evolutionary
foundation of familial relationships in hope of gaining a better understanding of the history
which has resulted in the biological patterns which these widespread parasites display today.

MATERIALS AND METHODS

Synthetic by design, the infrastructure of this thesis is composed of this author's personal
observations gathered over the past 14 years. During this period copepods were collected
from fishes with particular attention being paid to the specific identity of the host and the
exact location of the copepods on the host. The bulk of these collections was taken from
fishes important to commercial and/or sport fisheries, and most of these were taken from
large oceanic gamefishes (both sharks and teleosts) caught in the western North Atlantic in
association with sportfishing tournaments and scientific research cruises. Specimens on loan from other personal and museum collections, as well as published information, were used to augment data from the author's collections.

Copepods collected by the author were generally fixed in 10 percent (v/v) buffered formalin and later transferred to 70 percent ethyl alcohol. For morphological studies, copepods were cleared and stained in lactic acid into which a small amount of lignin pink was dissolved, dissected using fine needle probes, and studied under a compound microscope using the wooden slide technique of Humes and Gooding (1964). Drawings of copepods were often made with the aid of a camera lucida.

Electron microscopy was used to augment observations made using light microscopy. No special preparations were used to fix specimens for electron microscopy. Prior to examination, specimens were critical point dried and sputter coated with gold using standard techniques.

To study the histological relationships between parasites and hosts, some copepods were fixed while still attached to host tissues. These samples were fixed in either 10 percent (v/v) buffered formalin or Bouin's fixative. In the laboratory, these samples were dehydrated through a graded ethyl alcohol series, embedded in paraffin wax, and sectioned (10 µm) using a rotary microtome. Staining was in Delafield's haematoxylin and eosin or Mallory's trichrome stain. Histological preparations generally followed the standard techniques found in Humason (1972).

A cladistic analysis (see Abbott et al., 1985) was used to produce a cladogram of phylogenetic relationships for the 18 families of siphonostomes parasitic on vertebrates. A character set detailing the siphonostome parasites of vertebrates was constructed from
personal observations and published data (for a list of species and collections examined during the phylogenetic analysis of this thesis see Appendix 1). To determine character state polarity, the outgroup concept was used (see Stuessy and Crisci, 1984). A composite outgroup consisting of the siphonostome families associated with invertebrates was used to determine character state polarity within the ingroup. When character states conflicted between outgroup candidates, the commonly accepted concept (e.g. see Boxshall et al., 1984; Huys and Boxshall, 1991) that evolution has proceeded within Copepoda primarily by oligomerization (i.e. an evolutionary trend seen as a reduction in the number of body segments or other structural segments) was used to select the outgroup state. No effort was made to resolve relationships among siphonostome families associated exclusively with invertebrates or among those with no known host affiliations. To arrive at a phylogeny that seemed to possess at least some hope of reflecting reality, the ancient nature of Siphonostomatoida and the evolution of parasitic lineages had to be considered. This resulted in championing assumptions that some lineages have undergone similar evolutionary trends (i.e. parallel evolution) regarding body tagmosis, appendage segmentation, and appendage armament. These trends are associated with functional considerations (i.e. analogous use rather than homologous relationship), and none of the conventions used in identifying them are new (see Kabata, 1979; Huys and Boxshall, 1991). The most parsimonious cladogram was sought from all those possible from the set of character data. Table 1 provides descriptions of the apomorphic character states used in this analysis which ultimately determined the presented phylogeny.

To evaluate evolutionary trends, developmental and ecological data gathered from personal field observations and published reports were considered in light of or mapped onto the interfamilial phylogeny of the siphonostomes parasitic on vertebrates or as appropriate onto published phylogenies detailing intrafamilial relationships. Mapping developmental and ecological data onto a phylogeny simply involves the appropriate placement of these
observations on the phylogeny of a natural group of parasites with the intentions of analyzing the historical connotations of the mapped information.

Terminology used throughout the text conforms mostly with that adopted by Kabata (1979), Lincoln et al. (1982), and Huys and Boxshall (1991).

BIOLOGY OF SIPHONOSTOME FAMILIES PARASITIC ON VERTEBRATES

Brief synopses are provided below of morphological, developmental, and ecological information most pertinent to the phylogenetic analysis and evolutionary consideration of the siphonostome families parasitic on vertebrates. These synopses are not intended to be thorough morphological diagnoses. Those interested in familial diagnoses for siphonostomes parasitic on vertebrates are referred to the following publications: Yamaguti, 1963; Kabata, 1969b, 1979; Ho, 1987.

Eudactylinidae Biology

Eudactylinidae contains ten genera (see Deets and Ho, 1988). A synapomorphy defining this family is unknown. However, most eudactylinids differ from other siphonostome parasites of vertebrates by possessing a fifth pair of thoracic legs associated with a free thoracic segment rather than being incorporated into a genital complex (i.e. a body region formed by the fusion of the fifth pedigerous segment and the genital somites). Some eudactylinid genera exhibit cuticular flaps of varying shapes and sizes on the general body surface and/or appendages (e.g. Eudactylinodes Wilson, 1932, Eudactylina van Beneden, 1853, Jusheyus Deets and Benz, 1987). However, these flaps are not diagnostic for Eudactylinidae because
they are not universally possessed throughout the family (e.g. Protodactylina Laubier, 1966, Bariaka Cressey, 1966, Nemesis Risso, 1826, Carnifossorius Deets and Ho, 1988, Eudactylinopsis Pillai, 1968, Eudactylinella Wilson, 1932, Heterocladius Deets and Ho, 1988). Except in Carnifossorius (see below) body segmentation anterior to the genital region is conservative, with the cephalothorax incorporating the first pedigerous segment followed by four free pedigerous segments. Thoracic legs one-four are biramous, each ramus with two or three segments. Although vestigial, the fifth legs are large relative to those of other siphonostome parasites of vertebrates. Following the genital region is an abdomen consisting of one to four segments. First antennae exhibit 5 to 18 often ill-defined segments. The first antennae of Eudactylinodes and Eudactylina display large claws on the second segment and geniculate flexion (see Kabata, 1979; Deets and Ho, 1988) and probably assist in grasping the host. A rostrum occurs ventrally on the cephalothorax between the first antennae of several eudactylinids. In Eudactylina the rostrum consists of a basal plate with a posteroventrally directed tine (Kabata, 1979) while in Carnifossorius it consists of a basal plate only (Deets and Ho, 1988). Eudactylinid maxillipeds vary in shape between genera (see Kabata, 1979), with those of adult females generally ranging from subchelate to chelate. Sexual dimorphism is rather limited in Eudactylinidae (Fig. 1), and is often most pronounced in the maxillipeds (typically subchelate in males (see Kabata, 1979)) and thoracic legs (often more robustly armed and ornamented in males, including both longer setae and spines and greater density of pinnae (see Kabata, 1979; Deets and Benz, 1987; Deets and Ho, 1988)).

The first antenna of male Eudactylinella alba Wilson, 1932 exhibits a curious geniculate terminus which possibly assists in grasping the female during copulation.

Two eudactylinid genera display striking forms. Jusheyus is notable because its first thoracic segment bears dorsolateral styliform projections, and by possessing a genital somite rather than a genital complex. Jusheyus is also unusual because it has short multiseriate egg sacs containing round eggs.
The **Carnifossorius** adult female displays a greatly elongated cylindrical body with a cephalosome (i.e. the anterior portion of the body consists of five cephalic plus the maxilliped bearing somites) followed by an expansive first pedigerous segment, pedigerous segments two-four, a genital complex incorporating the fifth pair of legs, and an abdomen. Together these characteristics make *Carnifossorius* the most unusual member of Eudactylinidae. The modified habitus of *Carnifossorius* appears well-suited to its mesoparasitic lifestyle which is unique among eudactylinids. **In situ**, the adult female is buried to about the level of the first thoracic legs (a distance representing 20 percent of her length) in the interbranchial septa of her guitarfish host (*Rhina ancylostoma* Bloch and Schneider, 1801). The massive anteriorly projecting chelate maxillipeds apparently serve a primary role in attachment, as the straight tubular body itself does not seem totally capable of this function. Although males are currently undiscovered, they probably are ectoparasitic, more mobile, and exhibit relatively smaller and less modified bodies than females.

The phylogeny provided by Deets and Ho (1988) serves as a working hypothesis for systematic and ecological studies of Eudactylinidae. Reductions in the number of abdominal segments, in appendage segments, and in the number of armature elements associated with appendage segments was proposed (Deets and Ho, 1988) as an evolutionary process within Eudactylinidae and was generally corroborated by other seemingly independent morphological changes.

As indicated by extant taxa, Eudactylinidae appears to have originated on elasmobranch fishes and throughout its history has at least once invaded teleosts (see Deets and Ho, 1988). Mapping ecological characters onto the phylogeny of Deets and Ho (1988) shows that ectoparasitism is the predominant and primitive lifestyle within the lineage and that mesoparasitism is a derived activity (Fig. 2). Without exception, eudactylinids are parasites
of the branchial and olfactory regions of their hosts. The olfactory sacs represent a secondarily acquired niche (Fig. 2). Preliminary data show that on the gills and within the olfactory sacs various eudactylinid species are conservative regarding specific attachment locations (Fig. 3; also see Benz 1980; Benz and Adamson, 1990).

Developmental data for Eudactylinidae is incomplete. Copulation posture of *Nemesis robusta* van Beneden, 1851 has been seen on several occasions (Wilson, 1932; Carli and Bruzzone, 1978; Benz and Adamson, 1990). During copulation males use their maxillipeds to grasp females in a manner similar to that in which both sexes grasp their hosts. Except as noted above for *Jusheyus*, eudactylinid egg sacs are straight and contain slightly compressed eggs that are arranged uniseriately. Only two papers contain reports on eudactylinid larvae (Wilson, 1922; Kabata, 1976), and both deal with an unremarkable nauplius stage.

**Kroyeriidae Biology**

Kroyeriidae contains three genera: *Prokroyeria* Deets, 1987, *Kroyerina* Wilson, 1932, and *Kroyeria* van Beneden, 1853. Although kroyeriids are easily identified by a combination of unexclusive characters (see Deets, 1987), a synapomorphy defining this family is unknown. Kroyeriids have a small dorsoventrally flattened cephalothorax incorporating the first pedigerous segment followed by three small free thoracic segments, a long tubular genital complex, and a small one- to three-segmented abdomen. First antennae are seven- to nine-segmented. Second antennae are chelate, a notable condition found elsewhere among siphonostomes only in Pennellidae and *Pseudohatschekia* Yamaguti, 1939 (a dubious member of Hatschekiidae (see Kabata, 1979)). Maxillipeds are subchelate and relatively unmodified. Thoracic legs one-four are relatively unmodified, biramous, trimerous, with right and left pairs connected by interpodal bars. Leg setae are well-developed and enable at
least some of these copepods to swim freely as adults (Benz, 1986; Benz and Dupre, 1987). A small degree of sexual dimorphism is seen in kroyeriids (Fig. 1), with males being smaller (mainly due to the smaller size of the genital complex) and displaying more densely pinnate setae (possibly indicating greater mobility).

In addition to the aforementioned shared but not unique characteristics, some kroyeriid genera exhibit interesting novelties. *Kroveria* species display a pair of dorsal stylets which articulate with the posterior of the cephalothorax via a ball and socket-type joint. These dorsal stylets can be moved and presumably assist in temporary attachment by propping these copepods against the gill lamellae in the face of respiratory water flow (Fig. 4; see also Benz and Dupre, 1987). The dorsal stylets are reminiscent of similar structures found on *Jusheyus* and male *Eudactylinopsis* (both Eudactylinidae). Dorsal stylets of *Kroveria* species, however, differ from the dorsal styliform projections of *Jusheyus* in that the latter project from the first free thoracic segment rather than the cephalothorax and they do not articulate via a well-developed ball and socket joint (see Deets and Benz, 1987). However, Deets and Benz (1987) noted that the body segmentation of *Jusheyus* was difficult to interpret, and that *Jusheyus* may possess a cephalosome rather than a cephalothorax. Should this be true, the dorsal styliform projections of *Jusheyus* could be interpreted as an ancestral state to the dorsal stylets of *Kroveria*. Unfortunately comparison of the lateral cephalothoracic spines of male *Eudactylinopsis* to the dorsal stylets of *Kroveria* is prevented by a somewhat superficial description of *Eudactylinopsis* and a lack of study material. Although their exact attachment location has not been documented, *Eudactylinopsis*, like *Kroveria* species, resides on the gills of an elasmobranch (Pillai, 1968). The presence of lateral cephalothoracic spines in male *Eudactylinopsis* could represent a convergence with *Kroveria* analogously serving a temporary attachment role linked to the greater mobility and less powerful attachment appendages of *Eudactylinopsis* males versus females. This
conjecture is supported by the observation that female *Eudactylinopsis* have chelate maxillipeds which appear more powerful than the subchelate maxillipeds of the males.

*Kroveria* species also display interpodal stylets on the interpodal bars of legs one-four. These stylets, which do not articulate but which can be erected by movements of the interpodal bars, seem to provide a series of paired ventral tines that could be used like the dorsal stylets to prop these copepods against the host substrate in the face of water flow.

*Prokroyeria* and *Kroeyerina* display a pair of rostral processes at the anterior of the cephalothorax (see Deets, 1987). These processes are rudimentary in *Prokroyeria* and are most developed in the lineage of *Kroeyerina* infecting sharks, where they form two closely applied upturned horns (see Deets, 1987). The function of these structures is unknown. However, each of the two *Kroeyerina* lineages (one infecting batoids the other infecting sharks) has distinctive second antennae (Deets, 1987). The chelate second antennae of kroyeriids serve as the primary attachment appendages (Fig. 4), and possibly the dissimilar second antennae of these two lineages reflect differences in modes of attachment and that the enlarged rostral processes of the shark infecting lineage are somehow associated with these attachment differences.

All kroyeriids infect chondrichthyan fishes. *Prokroyeria* and all *Kroveria* species except *K. caseyi* Benz and Deets, 1986 inhabit (respectively) the gill lamellae of chimeras and sharks, while *Kroeyerina* species reside between the olfactory lamellae of elasmobranchs. The branchial chambers and olfactory sacs of chondrichthyans are quite similar environments (see below), each being composed of an orderly arrangement of narrowly spaced epithelial lamellae between which water flows in a one-way pattern (Benz, 1984, in preparation). The long thin kroyeriid habitus conforms well to such tight environments (Fig. 4).
Kroverya caseyi is unusual among kroyeriids in that it is a mesoparasite (Benz and Deets, 1986). Up to 80 percent of these relatively gigantic adult females (some reaching 60.5 mm long) can be found tortuously buried in the interbranchial septa of their shark hosts (Figs 5 and 6). Both the dorsal styles and interpodal bars of K. caseyi seem relatively smaller (see Benz and Deets, 1986) than those of other congeneres. These observations lend added evidence of an attachment role for these structures in ectoparasitic kroyeriids. Kroyeria caseyi is most remarkable because it possesses the typical array of Kroyeria swimming and attachment structures even though they hardly seem necessary for a parasite that is so deeply embedded in its host. The K. caseyi male is relatively small and ectoparasitic. Presumably mating occurs prior to the growth period which ultimately transforms the female into its large mesoparasitic form.

Almost nothing is known of kroyeriid development. Egg sacs are straight and contain slightly compressed eggs arranged uniseriately. Benz and Deets (1986) gave a description of Kroyeria caseyi nauplii that hatched upon fixation of adult females. Carli and Bruzzone (1973) reported keeping newly hatched nauplii of K. carchariaeglauci Hesse, 1879 alive in the laboratory for three days.

Hatschekiiidae Biology

Hatschekiidae contains six genera: Hatschekia Poche, 1902 with 78 species, Prohatschekia Nunes-Ruivo, 1954 with six species, Congericola van Beneden, 1851 with three species, monotypic Pseudocongericola Yu, 1933, monotypic Bassettithia (Wilson, 1922), and monotypic Wynnowenia Boxshall, 1987. Uniting the family, male and female hatschekiids lack maxillipeds and possess second maxillae with bifid claws. The hatschekiid general habitus is more (e.g. Hatschekia gracilis Yamaguti, 1954) or less (e.g. H. cepolae Yamaguti,
1939) elongated and cylindrical in cross section. When body segmentation is distinct (e.g. *Wynnowenia*) the general habitus is composed of a cephalothorax incorporating the first pedigerous segment followed by up to three free thoracic segments, a genital complex, and an abdomen. When body segmentation is obscure the general habitus can range from a cephalothorax followed by an indistinctly segmented thoracic neck and trunk (e.g. *Hatschekia linearis* Wilson, 1913), to merely a cephalothorax and trunk (e.g. *H. modesta* Kabata, 1965). The location of the thoracic legs is important in delimiting body regions of indistinctly segmented species. First antennae are uniramous, three- to nine-segmented. Second antennae form unciform claws. Three to five pairs of thoracic legs may be present, existing as biramous multimerous, biramous unimerous, or vestigial structures (see Kabata, 1979, 1991; Jones, 1985; Boxshall, 1987). Egg sacs are straight and the slightly compressed eggs are arranged uniseriately. Males are generally similar to albeit smaller than females because of their relatively smaller genital complexes. Lacking maxillipeds, hatschekiid males use their second antennae to grasp females during copulation (see Jones, 1985).

Almost nothing is known of the life history of Hatschekiidae. *Congericola*. *Pseudocongericola*, *Bassettithia*, and *Wynnowenia* are all gill parasites of conger eels (Congridae) or pike conger eels (Muraenidae) found throughout the world's oceans (see Boxshall, 1987). *Prohatschekia* and *Hatschekia* are found on the gills of numerous teleosts, especially in marine waters of lower latitudes (see Yamaguti, 1963; Jones, 1985; Kabata, 1991).

**Pseudocycnidae** Biology

Pseudocycnidae contains three genera: *Cybicola* Bassett-Smith, 1898 with three species, *Pseudocycnoides* Yamaguti, 1963 with two species, and monotypic *Pseudocycnus* Heller,
A synapomorphy defining this family is unknown. The adult female is relatively long and cylindrical, often without well-defined segmental boundaries. The first pedigerous segment is incorporated into the cephalothorax, while the fourth and fifth leg bearing segments are amalgamated with the genital components to form a genital complex. The abdomen is small, sometimes with large posterolateral caudal rami (e.g. *Pseudocycnus*). First antennae are uniramous and often indistinctly segmented. Second antennae exhibit unciniform terminal claws, second maxillae are brachiform, and maxillipeds are subchelate. Three to five pairs of modified legs are present. Legs one and two are typically biramous and unimerous, with rami issuing stubby naked setae. Third legs are usually uniramous and unimerous, and fourth and fifth legs are often vestigial and represented by a small cuticular bump with a short spiniform seta. Egg sacs are straight, with compressed eggs arranged uniseriately. Males are generally similar to albeit smaller than females because of their relatively smaller genital complexes. *Pseudocycnus* males are notable in exhibiting a conspicuous lateral projection on each side of the genital complex bearing the flagelliform fourth legs.

Besides Wilson's (1922) report of *Cybicola buccatus* (Wilson, 1922) nauplii, nothing is known of the larval development of pseudocycnids. Family representatives are found throughout the world's oceans as gill parasites mainly of scombrids (Scombridae).

**Hyponeoidae Biology**

Hyponeoidae contains two monotypic genera: *Hyponea* Heegaard, 1962 and *Tautochondria* Ho, 1987. A synapomorphy defining this family is unknown. Adult female hyponeoids display a roughly rectangular cephalothorax incorporating the first pedigerous segment, and appear generally similar to lernanthropids. Unlike lernanthropids, however, hyponeoids
have a well-delimited thoracic neck and relatively large indistinctly segmented abdomens which bear lateral processes from their anterior portions. Between the cephalothorax and abdomen a relatively large genital trunk issues a number of blunt processes. First antennae are uniramous and indistinctly six-segmented. Second antennae are uniramous and form powerful curved claws. Second maxillae are brachiform and notable in that the brachium distally bears one spiniform seta. Maxillipeds are subchelate. Thoracic legs one (incorporated into the cephalothorax) and two (on the thoracic neck) are present as small biramous unimerous structures with spiniform setae. Egg sacs are spiral shaped with discoid eggs arranged uniseriately. Males are unknown.

Hyponeoids have only been collected on several occasions (Heegaard, 1962; Markevitch and Titar, 1978; Ho, 1987) and have been positively recorded from only two hosts; a barracudina (*Notolepis rissoi* (Bonaparte, 1841): Paralepididae: Iniomi) and the fangtooth (*Anoplogaster cornuta* (Valenciennes, 1833): Anoplogasteridae: Berycomorphi). Hyponeoids seem to be a deep-sea group parasitic on the gill filaments of teleost hosts (Ho, 1987). Nothing is known of their larval development.

**Lemnanthropidae Biology**

Lemnanthropidae contains seven genera: *Lemnanthropus* de Blainville, 1822 with 123 species, *Aethon* Krøyer, 1837 with four species, *Norion* von Nordmann, 1864 with two species, *Sagum* Wilson, 1913 with seven species, *Lemnanthropodes* Bere, 1936 with three species, *Lemnanthropinus* Do, 1985 with eight species, and monotypic *Lemnanthropsis* Do, 1985. The highly modified bilobate fourth legs of lemnanthropids are a synapomorphy unifying the family (see Ho and Do, 1985). The adult female cephalothorax incorporates the first pedigerous segment and typically folds ventrally along its lateral margins forming a trench
through which one host gill filament passes (Figs 7 and 8). In some species (e.g. *Lernanthropus chrysophrys* Shishido, 1898) the cephalothorax exhibits lateral processes. Behind the cephalothorax the large indistinctly segmented trunk may display lateral (e.g. *Lernanthropinus*), dorsal (e.g. *Lernanthropus, Aethon, Sagum, Norion*), or ventral (e.g. *Lernanthropodes*) plates which may be partially or entirely formed from the third pair of legs (see Ho and Do, 1985). The abdomen usually is small and obscurely one- or two-segmented. First antennae are uniramous, often indistinctly segmented, and sometimes display a parabasal flagellum (e.g. *Lernanthropus*). Second antennae and maxillipeds are powerfully subchelate. Second maxillae are brachiform with well-developed distal armament. First legs are small, biramous, and unumerous. Second legs are usually similar to the first, or with rami fused to the sympod (e.g. *Aethon*), or absent (e.g. *Norion*). Third and fourth legs are highly modified. The third legs are notable in that they sometimes are large ventrally directed structures together forming a trench in line with that of the cephalothorax through which one host gill filament passes (Fig. 7). Egg sacs are straight or coiled with discoid eggs arranged uniseriately. Male lernanthropids mainly differ from females in being smaller because of their relatively smaller genital complexes. Lernanthropid males also differ from females in that their cephalothoraxes are not as contoured to conform to the host's gill filaments, and in that the highly modified third legs are typically lobate or bilobate structures which project laterally from the body.

Although only one complete life cycle is known, developmental data for Lernaeopodidae are significant. Development in *Lernanthropus kroyeri* van Beneden, 1851 involves two nauplii, one infective copepodid, four parasitic copepodid, two preadult, and one adult stages (Cabral, 1983; Cabral et al., 1984). The life cycle is particularly important because it represents the first complete life cycle for a siphonostome parasitic on vertebrates which does not include a chalimus stage (i.e. a copepodid tethered to its host by a frontal filament issued from a frontal organ on the cephalothorax).
Lernanthropids have worldwide distribution on marine teleosts, and display relatively high levels of host specificity (see Yamaguti, 1963; Kabata, 1979; Ho and Do, 1985). They are exclusive gill parasites whose adult female habitus is uniquely modified to allow these sizable parasites to efficiently attach about the afferent and efferent arterioles of the gill filaments of their hosts (see Davey, 1980).

In a phylogenetic analysis of Lernanthropidae, Ho and Do (1985) presented a hypothesis of intrafamilial evolution which reduced hydrodynamic drag and increased security of the relatively large and sessile adult female. Ho and Do (1985) proposed a euryhaline origin on teleost fishes for Lernanthropidae sometime about the Cretaceous. This conjecture was based on two points: the presumed relationship between Lernanthropidae and Dichelesthiidae and the discovery of the dichelesthiid fossil Kabatarina Cressey and Boxshall, 1989 on a euryhaline teleost from lower Cretaceous deposits, and the euryhaline host relationship of one of the two most primitive extant lernanthropids (Ho and Do, 1985). However, the assumption that Kabatarina is more closely related to Lernanthropidae than it is to any other marine siphonostome is now open to serious question because recent data suggest that Hyponeoidae appears much like Lernanthropidae (see Ho and Do, 1985; Ho, 1987). Because of this it is possible that Lernanthropidae originated on marine teleosts prior to the Cretaceous.

**Dichelesthiidae Biology**

Dichelesthiidae contains three monotypic genera: extant *Dichelesthium* Hermann, 1804 and *Anthosoma* Leach, 1816, and extinct *Kabatarina*. A groove on the second maxilla delimiting the distal portion of the brachium from the calamus is the only unique feature unifying
Dichelesthidiidae (Cressey and Boxshall, 1989). The adult female dichelesthidiid cephalothorax incorporates the first pedigerous segment and is followed by three or four often indistinct thoracic segments, a genital complex, and a one- to three-segmented abdomen. Elytra can be present laterally on the second and third pedigerous segments (Dichelesthium), or dorsally on the second (Anthosoma) or third and fourth (Kabatarina) segments. First antennae are uniramous, composed of six (Dichelesthium and Anthosoma) or at least 20 (Kabatarina) segments. Second antennae are subchelate and retractile in Dichelesthium and Anthosoma, and very robust and nonretractile in Kabatarina. Second maxillae are brachiform with prehensile tips. Maxillipeds are subchelate, with an undivided shaft and robust corpus in Dichelesthium and Anthosoma, or a three-segmented shaft and relatively more slender corpus in Kabatarina. Kabatarina displays four pairs of biramous, multimerous thoracic legs. In Dichelesthium legs one and two are biramous and unimerous, and leg three is an unsegmented lappet. In Anthosoma legs one-three are subcircular aliform plates. Egg sacs are straight in Dichelesthium, loosely coiled in Anthosoma, and unknown in Kabatarina. Eggs are discoid and arranged uniseriately. Sexual dimorphism is minimal in Dichelesthidiidae. Typically males are smaller than females because of a relatively smaller genital complex (Fig. 1). Males also lack well-developed lateral or dorsal elytra, and sometimes (e.g. Anthosoma) exhibit thoracic legs in a somewhat less modified condition than females. Little is known of the larval development of dichelesthidiids. Kabata and Khodorevski (1977) have reported on a copepodid of Dichelesthium.

Anthosoma crassum (Abildgaard, 1794) is distributed throughout the world's oceans mainly on large pelagic sharks where it usually, but not always, attaches in the mouth between the teeth and in the branchial chamber along the gill arches (e.g. Wilson, 1932; Shiino, 1955; Lewis, 1966a). Dichelesthium oblongum (Abildgaard, 1794) is distributed in the North Atlantic, Mediterranean, and Adriatic and Black Seas, where it is a gill parasite of sturgeons (Acipenseridae). Although it has been found in fresh water on migrating sturgeons
it is considered a marine species (see Kabata, 1979). Fossil Kabatarina pattersoni Cressey and Boxshall, 1989 was discovered in northern Brazil in lower Cretaceous deposits (approximately 110 myo). These fossils were extracted from within the branchiocranium of the salmonoid fish Cladocyclus gardneri Agassiz, where they were presumably gill or buccal cavity parasites not unlike Dichelesthium and Anthosoma. Based on stratigraphy, Cressey and Boxshall (1989) speculate that these fossils were deposited in an estuarine environment. It is notable that during this period of earth's history Brazil was closer to Africa than it is now (Windley, 1984) and the contemporary range of Dichelesthium oblongum (see Kabata, 1979, 1988a) would have appeared smaller. This possibly indicates that continental drift is responsible for the present distribution of this species.

Pennellidae Biology

Pennellidae contains 20 genera (see Kabata, 1979; Castro and Bacza, 1985; Boxshall, 1986), and is unique within Siphonostomatoida because some of its members exhibit two host life cycles (Kabata, 1979).

Pennellid development begins according to a typical or slightly modified siphonostome plan. Developing eggs hatch, releasing either nauplii (e.g. see Sproston, 1942; Schram, 1979) or infective copepodids (e.g. see Perkins, 1983). The latter pathway shortens the free-living portion of the life cycle in that nauplius development occurs while the embryo is still within the shelter of the egg. Free swimming copepodids seek their intermediate hosts (or only host for monoxenous species), on which they pass through a series of three or four chalimus stages (Kabata, 1981; Perkins, 1983) tethered to the host by a frontal filament. During copepodid-chalimus development pennellids acquire their characteristic mouth tubes (Sproston, 1942; Rose and Hamon, 1953; Kabata, 1963; Ho, 1966a; Schram, 1979; Perkins,
1983). The pennellid mouth tube is notable because its labrum and labium become intricately fused to form a proboscis-like oral cone which is capable of telescoping extension (Boxshall, 1990; Castro and Baeza, 1991). Chalimus development results in the production of free swimming (i.e. not tethered by a frontal filament) adult males and untransformed adult females. At this point, copulation often takes place and in effect ends the male's usefulness. However, before death males may remain on the intermediate host, become free swimming in the water column, or occasionally swim to the definitive host without subsequent development (Kabata, 1958; Anstensrud, 1992). Adult males and untransformed adult females are relatively unspecialized. The first antennae typically display reduced segmentation or an otherwise reduced appearance relative to most members of Eudactylinae, Kroyeridae, Hatschekiidae, Pseudocycnidae, Hyponeoidae, Lernanthropidae, and Dichelestriidae. The second antennae are robust and chelate, and having been present in this form since the copepodid stage they have been the primary attachment organs during postnauplius periods lacking the frontal filament. Up to four pairs of setose swimming legs each connected by an interpodal bar may be present, their locations similar to those of adult kroyeriids. The untransformed adult female's cephalothorax is unusual because it lacks maxillipeds (Kabata, 1979). Untransformed females may also display mandibles with seemingly underdeveloped dentition (Kabata, 1967a; Schram, 1979; Castro and Baeza, 1986).

After attaching to the definitive host, female pennellids undergo a metamorphosis. This change is apparently prompted by insemination (Anstenstrud, 1990a) and results in an often monstrous fully transformed adult female that frequently has confused naturalists. In fact, pennellids were among the first recorded fish parasites, with such noted scholars as Aristotle and Pliny misinterpreting their taxonomic status and treating them as worms (Wilson, 1917).
The untransformed adult female attaches to the definitive host using its powerful chelate second antennae. Then in an unknown manner the tiny female burrows into its host usually, but not always, toward a specific target. Often the lumen of some organ or region is sought: the ventral aorta (e.g. see Kabata, 1967b, 1970, 1979; Grabda, 1991), the heart (e.g. see Kabata, 1967b, 1970; Grabda, 1991; Perkins, 1983), the eye (e.g. see Kabata, 1969a; Schram, 1979; Grabda, 1991; Anstensrud and Schram, 1988), or the visceral cavity (e.g. see Shiino, 1958; Ho, 1966b; Kabata, 1979; Grabda, 1991). Prior to or upon reaching its final destination, the female begins to metamorphose (i.e. continuous growth not involving a molt). Various body regions (e.g. cephalic, thoracic, genital, and abdominal) begin to allometrically enlarge (see Kabata, 1969a, 1979; Schram, 1979, 1980; Grabda, 1991; Perkins, 1983; Castro and Baeza, 1985, 1986). The true appendages do not enlarge during this growth phase and are soon dwarfed by the surrounding regions' often grotesque expansions. This process results in an almost unrecognizable adult female with a cephalothorax deeply buried within the host, and genital and abdominal regions trailing free from the host into the surrounding water (Fig. 9). Egg sacs (which may be straight or coiled, with discoid eggs arranged uniseriately) extend from the female's posteriorly located oviduct openings into the water. Depending upon the trajectory of penetration, the adult female may be straight or highly twisted. The cephalothorax of some genera develops lateral processes which assist in anchoring these often enormous parasites (Kabata, 1979). Many pennellids exhibit a relatively high degree of intraspecific phenotypic variation as a result of their allometric growth phase interacting with various hosts and attachment locations (e.g. Kabata and Wilkes, 1977; Kabata, 1979; Hogans, 1986, 1987a, 1987b, 1988; Castro and Baeza, 1988; Benz and Hogans, in press).

**Ophiolernaea** Shiino, 1958 is a particularly unusual pennellid genus. Overall, most of the growth centers of **Ophiolernaea** are conservative in their metamorphic expansion. However, the oral region undergoes an enormous growth phase producing a long proboscis-like
extension. As a result, the buccal orifice is far removed from the rest of the cephalothorax. The vermiform proboscis of adult female *Ophiolernaea* tortuously works its way throughout the viscera of its host (Grabda, 1991). *Ophiolernaea*'s need for such an extremely long oral region is unknown. However, it may be linked to the fact that the visceral cavity of fishes is a mass of relatively shifting tissues and is quite different from the relatively more solid and stable regions where other pennellids often live. Thus *Ophiolernaea* may periodically find its mouth in a void. Possession of a growing mouth tube would seem to ensure contact with host tissues in such an unstable environment and might be considered an adaptation to mesoparasitism of the visceral cavity. Incipient development of luxuriant oral regions can be seen in *Metapeniculus antofagastensis* Castro and Baeza, 1985 and some *Peniculus* von Nordmann, 1832 species (e.g., *P. elongatus* Boxshall, 1986).

Pennellids share several morphological features which appear important to their mesoparasitic lifestyle. For example, the diagnostic lack of maxillipeds by female pennellids seems compensated for in males, untransformed females, and superficially attached transformed females by the powerful second antennae. During parasitic larval stages, possession of both chelate second antennae and a frontal filament reduces need for maxillipeds to secure the host. In deeply embedded species the transformed female's general habitus itself provides additional attachment support. Maxillipeds are retained by male pennellids and are used during copulation (see Sproston, 1942; Schram, 1979; Perkins, 1983). The mouth tube of pennellids also seems to lend itself well to mesoparasitism. Once embedded in its definitive host, the female often may be so firmly surrounded by host tissue that elevating or depressing the mouth tube in typical siphonostome fashion might be impossible (see Kabata, 1974a, 1979; Boxshall, 1990). For pennellids, a telescoping mouth cone perhaps solves this problem. The allometric growth phase which results in mesoparasitic females is also notable because it reshapes the habitus so that the copepod's body is not only firmly anchored, but also so that it extends from the internal source of
nutrition to the external environment into which the offspring are shed. The ability to
traverse this expanse precludes the free swimming larvae from having to negotiate a
seemingly impossible journey. The allometric growth phase is considered (Kabata, 1979;
Boxshall, 1986) to be an addition to the pennellid ancestral life cycle.

Boxshall (1986) presented a cladogram of Pennellidae genera summarizing knowledge of
transformed adult females. Although only partially resolved, this phylogeny faithfully
reproduced earlier ideas of Kabata (1979) concerning major pennellid lineages. To update
Boxshall's (1986) cladogram, Metapeniculus Castro and Baeza, 1985 can be assigned to the
Peniculus-group. When ecological life history traits are mapped onto the cladogram they
suggest that mesoparasitism may have arisen from an ectoparasitic lifestyle within
Pennellidae (Fig. 10). As set forth by Kabata (1982) and graphically depicted by Boxshall's
(1986) cladogram, attachment of pennellids on the body and fins of fishes represents the
ancestral condition while attachment to the gills and into the lumen of internal organs
represents more derived lifestyles. Even relatively ectoparasitic pennellids (e.g. Peniculus
and Peniculisa Wilson, 1917 species) burrow somewhat into their hosts using their second
antennae as major attachment organs. This invasion initiates the proliferation of host tissues
surrounding the parasite which eventually assists in strengthening parasite attachment
(Kabata, 1979; Radhakrishnan and Nair, 1981). Although information concerning the larvae
of most pennellids is lacking, the use of two hosts may be another life history characteristic
that arose within the family (Fig. 10).

Pennellidae is successful in infecting the most phylogenetically diverse host array of all
siphonostome lineages, with hosts including mollusks, teleosts, and mammals. Whether
fishes or invertebrates represent the more derived condition regarding the use of an
intermediate host cannot be established based on current knowledge (see Fig. 10).
Evolutionarily, however, it seems ecologically significant that pennellids often infect tightly
schooling organisms (see Yamaguti, 1963; Kabata, 1979). This preference may have predisposed the lineage to sometimes use the same host species as both an intermediate and definitive host (e.g. see Anstensrud and Schram, 1988). Two host life cycles may have further been facilitated by the loose attachment and powerful swimming ability of larvae and young adults. It also seems significant that for many pennellids using different species as the intermediate and definitive hosts the intermediate host is often a schooling organism that serves as prey for the definitive host (e.g. *Pennella filosa* (L., 1758) and *P. instructa* Wilson, 1917 use squid as intermediate hosts and very often tunas and billfishes as definitive hosts; see Rose and Hamon, 1953; Kabata, 1979; Hogans *et al.*, 1985; Hogans, 1986). Such a predator-prey association between the definitive and schooling intermediate hosts would seem to assure close host juxtaposition for parasite transmission.

**Sphyriidae Biology**

Sphyriidae contains eight genera: *Sphyron* Cuvier, 1830 with two species, *Lophoura* Kölliker, 1853 with 12 species, *Tripaphylus* Richardi, 1878 with two species, monotypic *Opimia* Wilson, 1908, *Paeon* Wilson, 1919 with five species, monotypic *Periplexis* Wilson, 1919, monotypic *Paeonocanthus* Kabata, 1965, and monotypic *Norkus* Dojiri and Deets, 1988. Sphyriids are easily identified by a combination of characters (see Dojiri and Deets, 1988), however, a synapomorphy defining this family is unknown. Adult female sphyriids are all mesoparasites and display a loss of external segmentation (Fig. 1). The female habitus can be divided into three general regions. The anterior region may be a simple expansion (e.g. *Opimia, Periplexis, Paeonocanthus, Lophoura*) or a more complex structure with various protuberances (e.g. *Norkus, Paeon, Tripaphylus, Sphyron*). The anterior region is followed by a narrower cylindrical neck which may (e.g. *Norkus, Periplexis, Paeonocanthus, Lophoura*) or may not (e.g. *Paeon, Tripaphylus, Opimia, Sphyron*) display
some type of expansion presumably serving as a holdfast. The posterior region may either form a gradual expansion from the neck (e.g. *Paeon, Tripaphylus, Opimia*), a discoid shape (e.g. *Norkus*) or an ovoid shape (e.g. *Periplexis, Paconocanthus, Lophoura, Sphyrion*). A pair of posterior processes representing modified caudal rami is attached to the trailing portion of the posterior region and may be cylindrical (e.g. *Norkus, Paeon, Tripaphylus, Opimia, Paconocanthus*), transversely constricted (e.g. *Periplexis*), multiply cylindrical (e.g. *Lophoura*), or branching (e.g. *Sphyrion*). In situ, the cephalothorax and at least two free thoracic segments are embedded in the host with one thoracic segment and the genitoabdomen trailing free from the host.

Appendages of transformed sphyriid females are generally small. First and second antennae are primitively uniramous and biramous respectively and sometimes only represented by cuticular swellings (e.g. *Periplexis, Paconocanthus, Lophoura, Sphyrion*). The mandibles of most genera are unknown, however, those of *Norkus* display both primary and secondary teeth (Dojiri and Deets, 1988) and appear very similar to the mandibles of lernaeopodids (e.g. see Kabata, 1979). When present, the second maxillae may be long and indistinctly segmented (e.g. *Norkus*) or mere cuticular swellings (e.g. *Lophoura, Sphyrion*). Maxillipeds, when present, are subchelate (e.g. *Norkus, Tripaphylus, Opimia, Sphyrion*). Thoracic legs, represented as vestigial structures (e.g. *Opimia*), are rarely present. Sphyriid egg sacs contain spherical eggs arranged multiseriately.

Sphyriid males have a grub-like form (Fig. 1), and are similar to males found in the families Lernaeopodidae and Naobranchiidae. Developmental observations of Sphyriidae are few and detail only early and late life history stages. In *Paeon* and *Sphyrion*, nauplius stages are passed inside the egg, resulting in a copepodid being the first free-swimming larval stage (Wilson 1920, 1932; Jones and Matthews, 1968). It is noteworthy that two important features can be seen in the first copepodid stage of *Paeon* (see Wilson, 1932) and
**Sphyriion** (see Jones and Matthews, 1968): the coiled frontal filament, and the biramous second antennae. Based on observations of lernaeopodid development (see below) it is generally accepted that the highly modified adult female results from the metamorphosis of an untransformed larval or young adult stage. Observations of **Sphyriion** metamorphosis reveal a process of polyphasic growth of various body regions (this process was detailed by Kabata (1979) concerning Pennellidae).

Based on the phylogenetic analysis of Dojiri and Deets (1988), Sphyriidae consists of two clades. The *Tripaphylus*-clade (i.e. *Norkus, Paeon, Tripaphylus, Opimia*) infects Elasmobranchii while the *Sphyriion*-clade (i.e. *Periplexis, Paeonocanthus, Lophoura, Sphyriion*) infects Teleostei. The sphyriid phylogeny of Dojiri and Deets (1988) is interesting because it is almost entirely congruent with an independent phylogeny of these parasites' hosts. Dojiri and Deets (1988) mapped environmental life history traits of sphyriids onto their sphyriid phylogeny and noted two clade specific lifestyles. When records of this author (Benz, 1986) are added to the analysis of Dojiri and Deets (1988), members of the Elasmobranchii infecting *Tripaphylus*-clade are all seen as parasites of the olfactory and branchial chambers while species composing the Teleostei infecting **Sphyriion**-clade all penetrate the body musculature.

**Lernaeopodidae Biology**

Lernaeopodidae contains many genera and about 260 species. Lernaeopodids are found throughout the world's oceans on teleosts and chondrichthians. As a group they may infect all external surfaces of the host's body, including the gills, spiracles, and olfactory sacs. The salmincolaforms are notable lernaeopodids because they are the most successful siphonostome, yet only lernaeopodid, taxon which has invaded fresh water. Each lineage
within Lernaeopodidae exhibits a fair degree of host specificity (see Yamaguti, 1963; Kabata, 1979, 1981).

The habitus of postmetamorphosis lernaeopodid females consists of a cephalothorax and trunk (Fig. 1). The cephalothorax may range from long (e.g. *Clavella* Oken, 1816, *Clavellisa* Wilson, 1915) to almost nonexistent (e.g. *Nectobrachia* Fraser, 1920). Caudal rami and posterior fimbrate processes may be attached to the trunk (see Kabata, 1979). Egg sacs are usually allantoic in shape and contain round eggs multiseriately arranged. *Cryptova* Kabata, 1992 is unusual within the family in possessing a brood chamber formed by a modification of its posterior processes (Kabata, 1992). First antennae are uniramous. Second antennae are biramous and usually have a large one-segmented exopod. Mandibles are typically short and robust, and may exhibit both primary and secondary teeth. Second maxillae are the principal attachment appendages, and are usually elongated, fused at their tips, and inserted into a structure known as the bulla. The bulla is implanted into the host, and along with the second maxillae serves an anchoring role. This scheme is modified a number of ways throughout Lernaeopodidae (see Kabata, 1979), and a bulla does not always provide the ultimate attachment. For example, in *Dendrapta* Kabata, 1964, *Brianella* Wilson, 1915, and *Schistobrachia* Kabata, 1964 the bulla is present in a vestigial condition. In these taxa, the bulla is only used during the initial attachment to the host. Afterwards, the buried tips of the second maxillae sprout luxuriant branches which permanently anchor the parasite (see Kabata and Cousens, 1972). Lernaeopodid maxillipeds are subchelate, and thoracic legs are vestigial or absent.

The general habitus of lernaeopodid males is grub-like (Fig. 1). Overall, males are best envisaged as equivalent to their respective females prior to female metamorphosis (Fig. 1), and hence they are considered to represent a relatively primitive level of development. In considering Lernaeopodidae, Kabata (1979) divided males into three groups. In the first
group males exhibit a cephalothorax and genitoabdomen, the lengths of which may or may not be similar. In the second group males have highly reduced trunks which give them a bulbous appearance. In the third group males are somewhat polytypic and relative to the other two groups they appear to be intermediate forms. The appendages of all three types of male are relatively homogeneous. First antennae are uniramous. Second antennae are biramous. Mandibles, when known, are typically short and may exhibit both primary and secondary teeth. Second maxillae and maxillipeds are subchelate. Thoracic legs are vestigial or absent.

Life cycles are known for several species of Lernaeopodidae (e.g. see Zandt, 1935; Dedie, 1940; Wilkes, 1966; Shotter, 1971; Kabata and Cousens, 1973; Kawatow et al., 1980; Piasecki, 1989). In reviewing developmental programs of parasitic copepods, Kabata (1981) considered Lernaeopodidae to exhibit two types of life cycles. The first, exemplified by Salmincola californiensis Dana, 1852, possesses one nauplius stage that is passed through in the egg, followed by an infective copepodid stage, four chalimus stages, an adult male, and an untransformed adult female which metamorphoses into a fully transformed adult (see Kabata and Cousens, 1973). In this scheme, molts only exist between nauplius, copepodid, chalimus, and adult stages. The transition between the untransformed adult female and the definitive adult female proceeds as a gradual metamorphosis. The second type of lernaeopodid life cycle proposed by Kabata (1981) is exemplified by the Clavella-branch of Lernaeopodidae, wherein (see Shotter, 1971) the free-swimming nauplius molts into an infective copepodid which subsequently molts into a "pupa" (sensu Heegaard, 1947). The female pupa (herein regarded as an untransformed adult) gradually metamorphoses into a fully transformed adult without molting, while the male pupa requires little noticeable development to be considered fully mature.
Recently, Piasecki (1989) has challenged Kabata's (1981) view of two life cycles within Lernaeopodidae using two lines of reasoning. First, Piasecki (1989) considers Kabata (1981) to be in conflict with some reports of free-living nauplii in some Salmincola-type lernaeopodids. In particular, Piasecki (1989) cites Zandt's (1935) report of two nauplius stages in *S. coregonorum* (Kessler, 1868), stating that his own observations of this species corroborate Zandt's. Kabata (1976) suggested that some observations of free-swimming nauplii in Salmincola-type life cycles may have been made on larvae obtained under unnatural conditions. Piasecki (1989) reports his own observations of a very short-lived nauplius stage which may rupture and release the copepodid stage simultaneously with rupture of the egg sac. Piasecki (1989) contends that perhaps the proportion of hatching nauplii to "hatching" copepodids is variable, and that this proportion may shift depending upon environmental factors. Secondly, as evidence of a transition between Kabata's (1981) Salmincola- and Clavella-type life cycles, Piasecki (1989) cites a study by Kawatow *et al.* (1980) which reports only three tethered chalimus stages in *Alella macrotrachelus* (Brian, 1906), a member of a lernaeopodid lineage which according to Kabata (1981) should be expected to exhibit four chalimus stages. Complete life cycles of other lernaeopodids are needed to settle this issue, however, as discussed by Piasecki (1989), both Kabata's (1981) and Piasecki's (1989) ideas on lernaeopodids illustrate two apparent developmental trends. One is the abbreviation of the free-swimming nauplius stage, and the other is a shift from ecdysial growth (i.e. growth mainly achieved via the molting process) to interecdysial growth (i.e. growth mainly achieved without molting; *sensu* Piasecki, 1989). Both trends seem to have some adaptive significance concerning the efficiency with which copepods can infect active hosts such as fishes.

The bulla which lernaeopodids implant in the host is formed during later chalimus development from the frontal organ which had formerly provided the frontal filament (see Kabata and Cousens, 1973; Piasecki, 1989). Throughout parasitic larval development and
into adulthood, the second maxillae join to the anchoring organ, thus tethering parasite to its host. This system, therefore, is best regarded as the modification and incorporation of a larval characteristic into the adult life history. Direct attachment of the muscular and contractile second maxillae to the bulla enables lernaeopodoids with short cephalocollums (i.e. the portion of the cephalothorax from the first antennae up to but not including the second maxillae; sensu Piasecki, 1989) to pull their mouth tubes to the host substrate. This is not possible for the larval chalimus which often sways seemingly helpless at the end of a long (see Benz, 1991) frontal filament. As noted by Kabata (1979), some lernaeopodids increase their feeding range via possession of an elongated cephalocollum (e.g. Clavella).

The punctuated crawling style lernaeopodids use to move about during nontethered chalimus existence, as well as during untransformed female and adult male periods differs from the swimming style of many other copepods. As discussed by Kabata and Cousens (1973) locomotion is accomplished by an inchworm-like motion which can be divided into three phases. In phase I the cephalocollum stretches forward and is held to the host substrate by the hooks of the second antennae. In phase II the trunk loops forward, its caudal rami pinning it in place behind the maxillipeds. In phase III the cephalocollum contracts and maxillipeds are released. This results in a forward shift of the second maxillae and maxillipeds. When the second maxillae reach a position close behind the buccal region, their grasp along with that of the maxillipeds is reapplied. Next the second antennae disengage and the copepod has now cycled back to its original stance. This method of movement provides a strong stationary stance, secured to the host by both powerful second maxillae and maxillipeds. The security this stance provides is important for the male during copulation and for the female when implanting the bulla. Crawling provides these copepods fair wandering ability which plays an important role in both mate location by the male and permanent attachment location by the female (e.g. see Kabata and Cousens, 1973), and it possibly has facilitated the radiation of lernaeopodids into new niches on their hosts.
Naobranchiidae Biology

Naobranchiidae contains one genus, *Naobranchia* Hesse, 1863 with 34 species. The general habitus and appendages of *Naobranchia* females are similar to those of lernaeopodids. Naobranchiids are unique, however, because they secure themselves to their hosts by encircling a gill filament with their elongated, ribbon-like second maxillae (Fig. 8). Male naobranchiids display the grub-like form characteristic of lernaeopodid males. Kabata (1992) has recently reported that males may occur in one of three basic forms differing in the placement and orientation of the genitoabdomen on the trunk.

*Naobranchia* has a cosmopolitan distribution and is found on a wide variety of teleosts (Yamaguti, 1963). Almost nothing is known about development in Naobranchiidae. Ovoid eggs may be carried in multiseriate egg sacs or in brood sacs. A report by Wilson (1915) of an incompletely metamorphosed *Naobranchia lizae* (Krøyer, 1863) illustrates the manner in which the band-like second maxillae develop. Apparently each second maxilla elongates and upon encircling a host gill filament the tips fuse with the trunk independent of one another to complete the unique belt-like holdfast.

Tanyleuridae Biology

Tanyleuridae contains one monotypic genus, *Tanyleurus* Steenstrup and Lütken, 1861. *Tanyleurus* attaches to its host using its short fused second maxillae which are highly branched at their tips to form a holdfast. The cephalothorax is represented by a small tubercle on the trunk. The trunk is wide, and wraps ventrally from each side to form the bulk of an unusual habitus. The first antennae are small uniramous appendages which bear some general likeness to the first antennae of lernaopodids. The second antennae are
uniramous and seemingly highly modified. The first maxillae appear reduced into small uniramous structures armed with two apical setae that are constricted along their lengths much like those seen within Lernaeopodidae. Maxillipeds are absent, as are all traces of thoracic legs.

Attached *Tanypleurus* have only been reported from the gills of *Eumicrotremus spinosus* (Müller, 1777) (Cyclopteridae), *Lycodes reticulatus* Reinhardt, 1838, and *L. lavalaei* Vladykov and Tremblay, 1936 (both Zoarcidae) in the North Atlantic (Kabata, 1969b, 1988a). Kabata (1969b) references a report of two specimens taken from the stomach of a Greenland shark (*Somniosus microcephalus* (Bloch and Schneider, 1801)), which had probably been swallowed along with their host. Although developmental data are unknown for *Tanypleuridae*, the seemingly modified habitus of the ovigerous female suggests that a metamorphosis exists between an untransformed larval or young adult stage and the known adult female form. Egg arrangement is multiseriate with egg sacs curling in a dorsal direction and containing spherical eggs. Male tanypleurids have not been discovered.

**Dissonidae Biology**

*Dissonidae* contains one genus *Dissonus* Wilson, 1906 with 11 species (see Deets and Dojiri, 1990). The dissonid cephalothorax incorporates the first pedigerous segment and is modified in the form of a dorsoventrally flattened shield. Along the anterior border of this shield are a pair of flap-like frontal plates. Areas of the cephalothorax and frontal plates which contact the host often have a thin marginal membrane which appears to assist in sealing the cephalothorax to the host substrate. Dissonids have the usual complement of siphonostome appendages. The first antennae lie in close contact with the host. The claw-like second antennae and subchelate maxillipeds are the primary attachment appendages. Legs one-four
are biramous and trimerous. The fifth and sixth legs are vestigial and are located on the genital complex. Egg sacs are long and discoid eggs are uniseriately arranged. Disregarding the genital complex, dissonid males appear very similar to females. Males, usually have longer setae on their swimming legs and caudal rami than females, and these setae often appear to have denser arrays of setules.

Dissonus species are parasitic on elasmobranchs and teleosts. Almost nothing is known about the ecology of Dissonidae. Some species have been reported from the gills of their hosts, while others have been collected from the general body surface. In either case the exact location of infection has seldom been noted. Dissonus adults appear capable of swimming, based on the well-developed setae of their natatory legs.

Little is known about development in Dissonidae. According to Anderson and Rossiter (1969), Dissonus nudiventris Kabata, 1965 hatches as a relatively immobile nauplius which remains attached to the ruptured egg sac by its elongated balancers. Dissonus nudiventris possesses only one nauplius stage. This nauplius is unusual because it has unsegmented and unarmed first and second antennae, and mandibles. Anderson and Rossiter (1969) also reported no evidence of a frontal organ in what appears to have been the infective copepodid of D. nudiventris. It is notable that the present author has observed a frontal organ in adult female D. spinifer Wilson, 1906 which perhaps indicates the former presence of a frontal filament (see Anstensrud, 1990b; Piasecki and MacKinnon, 1993).

Pandaridae Biology

Pandaridae consists of 13 genera and 42 species. The only known synapomorphy for the family is the possession of distinctive maxillipeds with a squat corpus maxillipedis and a
distally displaced myxal region (Kabata, 1979). Except for the maxillipeds, the general morphology of pandarids is similar to that of dissonids and cecropids. Pandarids incorporate the first pedigerous segment into the cephalothorax, with pedigerous segments two-four sequentially separate. Although some genera possess conspicuous corrugated adhesion pads and adhesion surfaces (Fig. 11) these structures are found outside of Pandaridae as well (e.g. see Kabata, 1966a; Benz and Deets, 1987, 1988; Benz, 1989; Deets and Benz, 1988; Deets and Dojiri, 1989). A high degree of variation in both leg segmentation and leg armament exists within the family. Seemingly primitive genera (e.g. *Pagina* Cressey, 1964) tend to have biramous, multimerous legs with long densely pinnate setae. More derived genera (e.g. *Pandarus* Leach, 1816) generally display fusion of ramus segments and spiniform setae.

Variations in body form and leg structure among pandarids have prompted consideration that perhaps Pandaridae is composed of two clades (Cressey, 1967; Kabata, 1979; Dojiri, 1983). The *Dinemoura*-group (*sensu* Kabata, 1979) consists of species which have been reported to exhibit a relatively narrow second free thoracic segment without dorsal or lateral plates, second maxillae with a crista (i.e. a patch of setules or denticles distally on the brachium of the second maxilla), and relatively unmodified legs (see Cressey, 1967; Kabata, 1979; Dojiri, 1983). The *Pandarus*-group (*sensu* Kabata, 1979) consists of species which have been reported to exhibit a more solid looking habitus with a wider second free thoracic segment with lateral or dorsal plates, second maxillae with a distal clavus (i.e. a spine-like projection located distally on the brachium between the calamus and canna), and modified lamelliform legs (see Cressey, 1967; Kabata, 1979; Dojiri, 1983). Having examined 12 of 13 pandarid genera this author does not support that Pandaridae is composed of two clades. First, the decision to characterize legs as unmodified versus lamelliform is a rather arbitrary one. For example, Cressey (1967) characterized the legs of *Echthrogaleus* Steenstrup and Lütken, 1861 and *Dinemoura* Latreille, 1829 as lamelliform even though they are members of a group defined as possessing unmodified legs (see Cressey, 1967; Kabata, 1979; Dojiri,
Furthermore, some legs of *Nessipus* Heller, 1868 are very similar to those of *Pseudopandarus* Kirtisinghe, 1950 even though these two genera reside in different groups (see Cressey, 1967; Kabata, 1979; Dojiri, 1983). The presence of a crista versus a clavus also seems misleading. For one, this author has found pandarids with both crista and clavus (Fig. 12). Secondly, the clavus of some species appears to be composed of a twisted group of cuticular fibers which could represent tightly whirled setules of a crista (Fig. 12). The only character which legitimately separates the *Dinemoura* and *Pandarus* groups is the form of the second free thoracic segment. Cressey (1967) noted that when interpreting morphological features of pandarids, this family's wide range of lifestyles has to be considered. This author concurs, and suggests that the morphological variation seen among pandarid genera is graded and is functionally associated with a transition from more mobile to more sessile forms.

Adult female pandarids are incapable of efficient swimming, and as noted by Wilson (1907b) they move in an uncoordinated fashion apparently seeking a holdfast when removed from their hosts and placed in aquaria. However, the males of many pandarid species are excellent swimmers, and rival any caligid the present author has had opportunity to observe.

Pandarids are considered exclusive parasites of elasmobranchs, although a few records of individuals taken from teleosts exist (e.g. see Kabata, 1979). Pandarids are relatively host and infection site specific (see Benz, 1981, 1986; Rokicki and Bychawska, 1991), and are sometimes found in large clusters on their hosts (e.g. see Benz, 1981). The corrugated surfaces which these copepods often possess seem to allow them to match the fluted surfaces of the placoid scales of elasmobranchs, thus helping to secure them against the ceaseless water flow encountered as parasites of such active hosts. The cephalothorax of at least some pandarids is rimmed with a row of ventrally directed spines (Fig. 13) which along with the marginal membrane must assist in attachment. Some species which inhabit relatively rough
regions of the host studded with prominent scales possess only the ventrally directed spines (Fig. 13).

Pandarid second antennae are typically used as grapnels, and those of some species are capable of becoming deeply embedded in the host (Fig. 14). Likewise, the chelate maxillipeds can sometimes play a primary role in attachment, and in particular those of Pandarus species seem specifically designed to grasp the placoid scales of elasmobranchs (Fig. 15; see also Benz, 1992). Some pandarid species are capable of passive permanent attachment not requiring energy to maintain a grip. For example, adult female Perissopus oblongatus (Wilson, 1908) embed their toothed second antennae (Fig. 16) between the placoid scales and into the flesh of their shark hosts. Typically assuming a "handstand" position, it is difficult to understand how these copepods apply their mouth tubes to the host substrate. Interestingly, adult females of the closely related P. dentatus Steenstrup and Lütken, 1861 use their maxillipeds rather than second antennae as the primary organs of attachment by permanently cementing the expansive planar surface of the myxal pad to host placoid scales (Fig. 17). Given that the second antennae and maxillipeds of P. oblongatus and P. dentatus are so similar (Cressey, 1967), it is unknown why these apparent sister species have such dissimilar methods of attachment.

Developmental records of pandarids are incomplete. Wilson (1907b) briefly discussed and figured newly hatched nauplii of Pandarus and Nesippus apparently obtained from aquarium-held ovigerous females. Wilson (1907b) also described a Nesippus copepodid that had been attached by its second antennae to a gill filament of an Atlantic sharpnose shark (Rhizoprionodon terraenovae (Richardson, 1836)), and further discussed and figured three chalimus stages of Perissopus dentatus collected from smooth dogfish (Mustelus canis (Mitchill, 1815)). Not only are these last reports noteworthy as the first authenticated observations of pandarid chalimus stages, but they also are important because they noted the
structure of the pandarid frontal filament. Wilson (1907b) detailed the frontal filament as two broad flat parallel bands emanating from a quadripartite frontal organ. Wilson (1907b) further noted that each band was very short, and their attachment required the cephalothorax of the chalimus to lie in close host contact. Since Wilson's observations, some observers have reported pandarid frontal filaments (e.g. Shiino, 1963) while others have not (e.g. Lewis, 1964; Cressey, 1967, 1968). Most recently Benz and Last (in review) reported a short, thin, double stranded frontal filament in *Echthrogaleus torpedinis* Wilson, 1907. This corroborated Wilson's (1907b) observations of a multi-stranded tether in at least some pandarids, and it now seems likely that the short, thin pandarid frontal filament may be easily broken or overlooked by researchers. The general inability to identify pandarid chalimus stages probably has hindered identification of preadults. However, it is possible that several juvenile pandarids reported by Shiino (1954) and Hewitt (1967) may have represented these stages.

Lewis (1964) made an interesting discovery of what appeared to be copepodid stages of *Nesippus costatus* Wilson, 1924 encysted in the fins of several teleost species. Normally, *Nesippus* adults are ectoparasitic on sharks, and as noted above, Wilson (1907b) reported a *Nesippus* copepodid collected from a shark. The many observations of Lewis (1964), however, suggest that encysted *N. costatus* larvae did not represent unusual occurrences. The cysts surrounding these larvae were produced by the hosts and each had a small opening at one end through which the copepod's caudal rami protruded. Lewis (1964) hypothesized that such a position would allow the encysted larvae to respire anally. Lewis (1964) found evidence that molting occurred while larvae were encysted, but did not have enough study material to be confident in assigning specific stages to the four larval morphs he examined. No frontal filament was seen in these larvae, however, a quadripartite frontal organ was observed. Further study of the life cycle of *N. costatus* seems desirable as it possibly
represents a two host life cycle known elsewhere among the siphonostomes parasitic on vertebrates only in Pennellidae.

Cecropidae Biology

Cecropidae consists of five genera: *Luetkemia* Claus, 1864 with two species, and monotypic *Cecrops* Leach, 1816, *Orthagoriscicola* Poche, 1902, *Philorthagoriscus* Horst, 1897, and *Entepherus* Bere, 1936. A synapomorphy for Cecropidae is unknown. Although the second and third thoracic segments are fused in some cecropid species, this character is also seen in some pandarids (e.g. *Echthroaleus*). Like Dissonidae and Pandaridae only the first thoracic segment is incorporated into the cephalothorax in Cecropidae. Except for the maxillipeds, cecropid appendages generally resemble those seen among pandarids. Adult female cecropids are massive copepods that can reach at least 3 cm in total length. Their large size and reduced leg setae suggest poor swimming ability, and according to Wilson (1907b) they are relatively sessile on their hosts and somewhat uncoordinated when removed and placed in aquaria. The crypting and proliferation of host tissues often associated with cecropid infections (e.g. see Scott, 1892; Wilson 1907b; Grabda, 1973; Benz and Deets, 1988) supports Wilson's (1907b) remarks, as such pathologies require the presence of stationary parasites. Male cecropids are also relatively heavyset in comparison to other siphonostome males with dorsal shields (Fig. 1).

Cecropids are parasitic on batoids and teleosts. The ocean sunfish (*Mola mola* (L., 1758)) can harbor three cecropid genera which form a monophyletic group (see Benz and Deets, 1988). Cosmopolitan *M. mola* and its cecropid parasites, therefore, become an interesting species pattern which could have formed by either parapatric or sympatric speciation processes. The confused records describing the exact location of these copepods on the
ocean sunfish, however, do not allow either speciation process to be favored (e.g. cf. Wilson, 1907b and Wilson, 1932 concerning the distributions of Orthagorisciola muricata (Krøyer, 1837) and Philorthagoriscus serratus (Krøyer, 1863)). Benz and Deets (1988) noted that all cecropid hosts are epipelagic fishes, and it is possible that Cecropidae represents a taxon that constantly tests and periodically colonizes highly mobile oceanic hosts. Although no complete life cycle is known for Cecropidae, nauplius and chalimus stages have been observed (Wilson, 1907b; Grabda, 1973). The frontal filament of the chalimus is composed of two parallel bands (Wilson, 1907b; Grabda, 1973). Grabda (1973) observed that the chalimus of Cecrops latreillii Leach, 1816 uses its second antennae and maxillipeds in addition to its frontal filament to secure its host.

Trebiidae Biology

Trebiidae contains two genera: Trebius Krøyer, 1838 with 14 species, and monotypic Kabataia Kazachenko, Korotaeva and Kurochkin, 1972. Trebiids are superficially similar to other siphonostomes with cephalothoracic shields, however, their overall body plan uniquely consists of a cephalothorax incorporating the first two pedigerous segments, followed by two free pedigerous segments, a genital complex, and an abdomen. Trebiids, euryphorids, and caligid s share distinctive first maxillae whose rami are separated from one another. The endopod forms a robust projection and the exopod is a small cuticular bump with one-three setae. Kabataia differs from Trebius in possessing lateral plates on the first free pedigerous segment and in lacking a sternal furca.

Monotypic Kabataia is parasitic on teleosts while all 14 species of Trebius infect elasmobranchs (Kabata, 1979; Deets and Dojiri, 1989). Phylogenetic relationships within Trebiidae have not been established, however, Deets and Dojiri (1989) recently grouped
some **Trebius** species using various morphological characters. Few developmental data exist for **Trebiidae**. A chalimus stage of *T. caudatus* Krøyer, 1838 and what possibly were the first and second preadult stages of *T. exilis* Wilson, 1906a have been reported by Wilson (1907a).

**Euryphoridae Biology**

**Euryphoridae** contains five genera: **Euryphorus** Edwards, 1840 with two species, **Gloioptes** Steenstrup and Lütken, 1861 with 5 species, **Alebion** Krøyer, 1863 with 8 species, **Paralebion** Wilson, 1911 with two species, and **Tuxophorus** Wilson, 1908 with six species. Euryphorids are generally similar to other siphonostomes that possess cephalothoracic shields. They share with trebiids and caligids a two piece first maxilla. Euryphorids have only one free thoracic segment between the cephalothorax and genital complex, with the first three pedigerous segments and their legs incorporated into the cephalothorax.

A synapomorphy for Euryphoridae is unknown (see Dojiri, 1983). Kabata (1979) proposed the possession of paired dorsal aliform plates on the fourth leg-bearing segment of female euryphorids as a familial marker. However, Dojiri (1983) speculated that the dorsal plates of euryphorids perhaps were adaptations which hydrodynamically streamline or assist these copepods in attachment, and that their presence might be indicative of an environmental lifestyle rather than phylogeny. Dojiri (1983) further argued for the inclusion of euryphorid species within Caligidae based on the presence of aliform plates on the genital complexes and abdomens of some Caligidae members, stating that the presence of aliform structures should not carry any more taxonomic weight in one family versus another. Dojiri (1983) noted that the euryphorid **Paralebion elongatus** Wilson, 1911 does not exhibit well defined dorsal aliform plates on its fourth pedigerous segment but rather slightly inflated
joints where the fourth legs meet the body. Therefore, Euryphoridae and Caligidae share variable character mixes and are difficult to delimit.

The design of the cephalothorax and third pair of legs makes adult euryphorids capable swimmers and allows them to seal themselves to their hosts using suction (see discussion below). Euryphoridae has representatives infecting both sharks and teleosts, with *Euryphorus* seemingly preferring large scombrids, *Gloiopotes* seeking billfishes, *Alebion* and *Paralebion* infecting carcharhiniform sharks, and *Tuxophorus* parasitizing various nearshore and oceanic teleosts (see Yamaguti, 1963; Kabata, 1979). Euryphorids are usually found on the general body surface of their hosts. Some species parasitic on sharks exhibit very narrow niches as adults (Fig. 18).

Developmental data are incomplete for Euryphoridae. Wilson (1907a) stated that euryphorid nauplii are different from those of Caligidae regarding shape of the balancers (i.e. tapering in euryphorids and spatulate in caligids). However, Benz et al. (1992) noted that the balancers of the euryphorid *Paralebion elongatus* are spatulate in the first nauplius and tapering in the second nauplius. More importantly, Wilson (1907a) noted that a frontal filament was lacking from attached copepods of *Alebion glaber* Wilson, 1905. Instead, these larvae attached to their shark hosts using their powerful second antennae. Benz (1989) has corroborated Wilson's (1907a) observations by finding no evidence of a frontal filament in attached copepods of *A. lobatus* Cressey, 1970 (see Fig. 19).

Caligidae Biology

Consisting of at least two dozen genera and well over 300 species, Caligidae contains more species than any other siphonostome family. Like euryphorids, caligids have only one free
The thoracic legs are relatively uniform throughout Caligidae (Kabata, 1979, 1988b). Although some adult female caligids seem to prefer a relatively sessile existence (Fig. 20), many observers have commented on this group’s swimming abilities. Kabata and Hewitt (1971) detailed the role of various appendages associated with caligid locomotion. The first and second legs work together in antagonistic fashion to produce a propulsive thrust of water which is expelled from under the cephalothorax through the posterior sinuses. Water is recruited for locomotion from below the frontal plates in the anterior region of the cephalothorax. Dorsoventral flexion of the trailing portions of the body (genital complex, abdomen, and caudal rami) apparently are responsible for initiating dorsoventral movements.

Kabata and Hewitt (1971) also described settling movements of caligids. Settling movements are important to copepods attempting to maximize attachment efficiency by locating and securing an optimal resting site. The third pair of legs and their interpodal plate play an important role in the process of settling and attachment because together they allow the cephalothorax to be sealed to the host substrate. The second maxillae assist in crawling and lateral body movements.

Tines associated with the second antennae, postantennary processes, sternal furca, and swimming legs likely assist in anchoring caligids in the face of the forward-aft water flow associated with a swimming host. In addition to these structures, some caligids possess a pair of suctorial lunules which appear to be an elaboration of the marginal membrane.
associated with the frontal plates (see Kabata, 1979). The lunules seem to provide the anterior portion of the cephalothorax a means of attachment which might assist the copepod when it releases suction from beneath its cephalothorax and actively skitters over its host.

Caligids use a structure known as the strigil to rasp free bits of host tissue to be conveyed deeper into the mouth tube by the mandibles (Kabata, 1974a). To date the strigil has only been identified from Caligidae and some members of Euryphoridae (see Kabata, 1979; Dojiri, 1983; Benz et al., 1992).

Although caligid species have some representatives infecting elasmobranchs (see Yamaguti, 1963) and invertebrates (see Ho, 1980; Ruangpan and Kabata, 1984), they are predominantly parasites of teleosts, and like most siphonostomes they exhibit a fair degree of host specificity (see Yamaguti, 1963; Kabata, 1979). Caligids can be found virtually anywhere over the general body surface of potential hosts (olfactory, buccal, and branchial cavities included), and upon close study particular species are often seen to be relatively specific concerning infection site of the adult female (Fig. 20; see also Anstensrud, 1990c, 1990a).

Because caligids cause disease on schooling fishes of considerable commercial importance (see Wootten et al., 1982; Roth et al., 1993) it is not surprising that their life cycles are better understood than those of other siphonostomes possessing dorsal shields. Within Caligidae, four species of *Lepeophtheirus* von Nordmann, 1832 (see Lewis, 1963; Voth, 1972; Boxshall, 1974b; Johnson and Albright, 1991a) and seven species of *Caligus* Müller, 1785 (see Gurney, 1934; Heegaard, 1947; Hwa, 1965; Izawa, 1969; Kabata, 1972; Caillet, 1979; Ben Hassine, 1983) have had all or most of their developmental stages identified. These studies, along with numerous others less completely detailing development, depict a standard life cycle for Caligidae consisting of ten stages: free swimming nauplius 1 and 2, infective copepodid, chalimus 1-4, preadult 1 and 2, and adult.
Like all chalimus stages, those of Caligidae are tethered to their hosts by a frontal filament extruded from a frontal organ. Several reports of caligid preadult stages attached by a frontal filament have conflicted with a majority of others depicting preadult and adult stages as free ranging (e.g. see Lewis, 1963; Kabata, 1972, 1981; Anstensrud, 1990b; Johnson and Albright, 1991a). Recently, however, Anstensrud (1990b) observed that just prior to molting, the preadult produced a frontal filament which tethered it throughout the process of ecdysis. Soon after molting, once the new cuticle had hardened, the frontal filament was broken and prehension was facilitated by typical adult mechanisms (Anstensrud, 1990b).

Anstensrud (1990b) observed that in *Lepeophtheirus pectoralis* (Müller, 1777) the preadult frontal filament was composed of two very thin twisted strands. These strands arose from a frontal organ formerly considered to have a chemosensory function (Kabata, 1981), or possibly no function at all (Oldewage and Van As, 1989). Anstensrud (1990b) stated that given the brief existence and fragile nature of these frontal filaments it is understandable why they have not often been observed. Perhaps the presence of the rugose frontal organ can be used to predict the former or future presence of frontal filaments.

**SIPHONOSTOME RELATIONSHIPS**

Analysis of the 18 siphonostome families parasitic on vertebrates resulted in one most parsimonious cladogram supported by 30 characters (Fig. 21 and Table 1). This phylogeny was based on the concept that the siphonostome families parasitic on vertebrates form a natural (i.e. monophyletic) group. Important (but not essential) to this concept are the ideas that Siphonostomatoida is monophyletic, and that the siphonostomes parasitic on vertebrates
were derived from the siphonostomes of invertebrates. These topics will be discussed briefly before the phylogeny for the siphonostomes parasitic on vertebrates is detailed.

Monophyletic Siphonostomatoida

Thorell (1859) proposed a classification for copepods that grouped taxa independent of ecological characteristics (i.e. free-living versus parasitic). This classification was important to the study of Copepoda, for without pretension founded upon ecological pigeonholing, subsequent phylogenetic analyses based on morphological and anatomical characters suggest a multiple origin of parasitism as a copepod lifestyle (see Bocquet and Stock, 1963; Kabata, 1979; Ho, 1990; Huys and Boxshall, 1991; Stock, 1991).

Recently none have seriously challenged the monophyly of Siphonostomatoida (see Kabata, 1979; Huys and Boxshall, 1991; Stock, 1991). Marcotte (1982) argued, albeit very tentatively, for at least a diphyletic Siphonostomatoida based on general differences in the oral cone between siphonostomes associated with invertebrates and those parasitic on vertebrates, as well as on body segmentation and several appendage characteristics. However, these differences were not explicitly explained, and no consideration was given to the possibility that evolution within the order had produced the taxonomic diversity observed today. Such shortcomings render Marcotte’s (1982) di- or polyphyletic Siphonostomatoida highly speculative and founded solely on the vast and often confusing variation among these copepods. In fact, as set forth by Thorell (1859), membership within the order is best demonstrated by the possession of a tubular mouth (oral cone) composed of anterior and posterior lips (respectively the labrum and labium) and containing styliform mandibles (Fig. 22).
Monophyly of Siphonostomes Parasitic on Vertebrates

Interfamilial relationships among siphonostomes are ill-defined (see Huys and Boxshall, 1991). Progress in defining these relationships has been hindered by a relative lack of knowledge about the siphonostomes associated with invertebrates, and by the difficult to interpret diversity of the siphonostomes parasitic on vertebrates. However, because siphonostome families are almost always exclusively associated with either invertebrate or vertebrate hosts it has generally been assumed that siphonostomes parasitic on vertebrates might form a derived and monophyletic group (see Huys and Boxshall, 1991). Huys and Boxshall (1991) characterized this lineage by a number of features, none of which are both exclusive to and universally possessed throughout the group.

The lack of any clear synapomorphy unifying siphonostome families parasitic on vertebrates has periodically prompted discussions of polyphyly (Kabata, 1979; Cressey and Boxshall, 1989). Kabata (1979), for example, briefly considered the ectoparasitic siphonostomes of fishes to perhaps have been derived from siphonostome associates of invertebrates exhibiting depressed cephalothoraxes and podoplean design (i.e. forms in which the main body articulation exists between the fourth and fifth pedigerous somites). However, Kabata (1979) did not mention the possible origins of fish-parasitic families such as Eudactylinidae, Kroyeriidae, Hatschekiidae, Pseudocycnidae, Dichelesthiiidae, Hyponeoidae, and Lernanthropidae, all of which are not markedly depressed dorsoventrally and yet which seem in many respects to be relatively primitive among the siphonostomes parasitic on vertebrates. Kabata (1979) suggested that Pennellidae might have arisen from Megapontiidae-like ancestors based on the presence in these families of a peculiar mouth cone. However, recent comparative studies of the siphonostome oral cone (Boxshall, 1990)
reveal the mouth tube of Megapontiidae to differ fundamentally from that of Pennellidae, although one possibly could speculate on the evolution of the latter from the former.

The idea that siphonostomes parasitic on vertebrates form a monophyletic group is endorsed in this thesis based on four characters. The first character (character 1 of Table 1 and Fig. 21) unifying the siphonostomes parasitic on vertebrates is the presence of a prominent row of teeth along one side of the mandible (e.g. see Fig. 22). The mandibles of siphonostomes associated with invertebrates often have very small teeth and/or teeth which appear in a short row at the mandible’s apex. This characteristic is not clear-cut. Some siphonostomes parasitic on vertebrates belonging to highly modified families possess mandibles with seemingly reduced dentition (e.g. some Pennellidae), or may even lack mandibles (e.g. some Sphyriidae). Antithetically, some siphonostomes associated with invertebrates possess relatively stout mandibles with somewhat larger teeth that appear concentrated on one side of the apex (e.g. Dirivultidae).

The second character unifying the siphonostomes parasitic on vertebrates is the presence of second antennae lacking exopods (character 2 of Table 1 and Fig. 21). This character also is not clear-cut. The one-segmented exopod characteristic of the siphonostomes associated with invertebrates may be small or virtually absent (as in Dirivultidae and Dinopontiidae respectively), or sometimes completely absent (e.g. Nanaspididae, Nicothoidae and Micropontiidae). To the contrary, the closely allied families Sphyriidae, Lernaepodidae, and Naobranchiidae (all parasitic on fishes) possess second antennae with well-developed one-segmented exopods. These second antennae, however, appear to function in both important sensory and attachment roles associated with the highly modified larval and adult lifestyle characteristic of these copepods (Kabata, 1979). This functional reliance on the second antennae might be responsible for the maintenance or evolution of this character.
The third character unifying the siphonostomes parasitic on vertebrates is the possession of relatively long uniseriate egg sacs (character 3 of Table 1 and Fig. 21). This characteristic is also not clear-cut, with *Jushevus* (Eudactylinidae), Sphyriidae, Lernaeopodidae, Naobranchiidae, and Tanypleuridae displaying multiseriate or otherwise modified eggs sacs. As discussed below, the multiseriate egg sacs seen among the siphonostome associates of invertebrates and the above mentioned taxa are probably nonhomologous.

The last character unifying the siphonostomes parasitic on vertebrates is the absence of the mandibular palp (character 4 of Table 1 and Fig. 21). This absence is considered a loss and, therefore, implies that the siphonostomes parasitic on vertebrates were derived from siphonostomes associated with invertebrates. Huys and Boxshall (1991) considered the absence of a mandibular palp to be the most robust character separating the siphonostomes parasitic on vertebrates from those associated with invertebrates. However, this character is hardly clear-cut and actually appears to be the weakest of the four characters presented herein separating the two groups. Although the absence of a mandibular palp is a characteristic shared by all siphonostome families parasitic on vertebrates, it is also absent on many siphonostome families associated with invertebrates (e.g. Brychiopontiidae, Calverocheridae, Cancerillidae, Dinopontiidae, Dirivultidae, Dyspontiidae, Ecbathyriontidae, Entomolepidae, Megapontiidae, Myzopontiidae, Nanaspidae, Nicothoidae, Saccopsidae, Spongionizontidae, and Stellicomitidae). It is not known whether this commonality represents convergence or homology among these taxa and the siphonostomes parasitic on vertebrates.
Interfamilial Relationships Among Siphonostomes Parasitic on Vertebrates

Although cladistic analysis of the 18 families of siphonostomes parasitic on vertebrates did not fully resolve the phylogenetic relationships among these taxa, several well-defined lineages were identified (Fig. 21) along with a general trend indicating the evolution of morphological characteristics which seem to increase the efficiency of attachment and in some cases open new niches.

Eudactylinidae has generally been considered the most primitive siphonostome family parasitic on vertebrates (Kabata, 1981; Huys and Boxshall, 1991). In this thesis Eudactylinidae's primitive status is based on its members possessing fifth thoracic legs which are free from the genital somite (see character 5 of Table 1 and Fig. 21). Because this characteristic is shared with many siphonostome associates of invertebrates it is a sympleisiomorphy rather than a synapomorphy considering the cladogram. Although virtually all published considerations of the evolutionary position of Eudactylinidae mention the importance of a free fifth thoracic segment as a primitive characteristic (e.g. see Kabata, 1979; Deets and Ho, 1988; Huys and Boxshall, 1991), it should be noted that the formation of a genital complex may have independently occurred more than once among the siphonostomes infecting vertebrates and that endorsement of such a parallelism could place Eudactylinidae in an unresolved relationship with other relatively underived taxa (see Fig. 21).

Although some members of Eudactylinidae exhibit other seemingly primitive characteristics such as geniculate condition of the male first antennae (see Huys and Boxshall, 1991), these characteristics are possessed by only a few species within the family and, therefore, they were not chosen for inclusion in this dissertation's phylogenetic analysis. The multiseriate egg sacs of Jusheyyus are considered a reversal within Eudactylinidae from
the uniseriate condition used to help delimit the siphonostomes parasitic on vertebrates
(character 3 of Table 1 and Fig. 21).

Progressing up the cladogram, Kroyeriidae is set apart from surrounding taxa by its chelate
second antennae (character 6 of Table 1 and Fig. 21), a homoplastic character shared with
Pennellidae and Pseudohatschekia. Kroyeriidae is further separated from Eudactylinidae
based on its fifth legs being incorporated into a genital complex (character 5 of Table 1 and
Fig. 21). Kroyeriidae is delimited from families Hatschekiidae, Pseudocycnidae,
Hyponeoidae, Lernanthropidae, and Dichelesthiidae based on its unmodified fourth legs
which are connected by well-developed interpodal bars and which are located on well-
defined free thoracic segments (see character 7 of Table 1 and Fig. 21). Kroyeriidae is
delimited from taxa further up the cladogram by its lack of a frontal organ associated with a
larval frontal filament (see character 12 of Table 1 and Fig. 21) and by its relatively highly
segmented first antennae (see character 13 of Table 1 and Fig. 21). It should be noted that
virtually nothing is known about the development of kroyeriids and that the absence of a
frontal organ is based on examinations of adults rather than larvae.

Together, families Hatschekiidae, Pseudocycnidae, Hyponeoidae, Lernanthropidae, and
Dichelesthiidae form the dichelesthiiform assemblage (see Fig. 21). These five families are
grouped together based on their possessing fourth thoracic legs which are highly modified or
completely lost (character 7 of Table 1 and Fig. 21). A superficially similar characteristic is
seen within the highly derived lernaeopodiform lineage (i.e. Sphyriidae, Lernaeopodidae,
Naobranchiidae, and Tanypleuridae) in that all thoracic legs of lernaeopodiforms are vestigial
(see character 16 of Table 1). Because dichelesthiiforms and lernaeopodiforms
morphologically appear so distinct and because reduction in leg segmentation is a
phenomenon seen within a number of siphonostome lineages, this similarity is not
considered a homoplasy, but rather two distinct characters. It should be noted that the fossil
dichelesthiid **Kabatarina** possesses four pairs of possibly unmodified biramous legs (see Cressey and Boxshall, 1989), and that its inclusion in the cladogram as a dichelesthiid might require some to consider character 7 more exclusive, resulting in Dichelesthiiidae dropping into a more immediate association with Kroyeriidae. This convention has not been followed for two reasons. First, the relationship of **Kabatarina** to other dichelesthiiids is questionably based on only one fine characteristic (a groove on the second maxilla delimiting the distal portion of the brachium from the calamus; see Cressey and Boxshall, 1989). Of course, the transfer of **Kabatarina** into some other family would only serve to alter which family would fall into closer relationship with Kroyeriidae. More importantly, the leg segmentation of **Kabatarina** is somewhat uncertain (see Cressey and Boxshall, 1989) and it seems very possible that it may represent a reduction from the biramous, trimerous condition seen in Kroyeriidae. This author would like to make notice of the four pairs of swimming legs possessed by all kroyeriids as being primitive and notably different from the conditions seen among families Hatschekiidae, Pseudocycnidae, Hyponeoidae, Lernanthropidae, and Dichelesthiiidae, and yet similar to that seen among untransformed pennellids and caligiforms (i.e. Dissonidae, Pandaridae, Cecropidae, Trebiidae, Euryphoridae, and Caligidae). This primitive condition is also shared with underived eudactylinid genera such as **Protodactylina** and **Bariaka** (see Deets and Ho, 1988) and is considered a sympleisiomorphy in this analysis. It certainly is possible, however, that a trend defined as the reduction of the first four pairs of legs from a biramous, trimerous, setose state with left and right pairs connected by well-developed interpodal bars may have occurred more than once among these families. If this were so concerning the entire dichelesthiiiform assemblage then character 7 would have to be abandoned and the polytomy that it supported would then additionally include Kroyeriidae (see Fig. 21).

Dichelesthiiiforms are also separated from Pennellidae and other taxa further up the cladogram (i.e. caligiforms and lernaeopodiforms) by lacking a frontal organ associated with
the larval frontal filament (see character 12 of Table 1 and Fig. 21) and by generally having first antennae with a relatively high number of segments (see character 13 of Table 1 and Fig. 21). This last character is not clear cut, as among some seemingly modified dichellesthiiiforms the segmentation of the first antennae may be indistinct (see Kabata, 1979). It should also be remembered that developmental information is almost completely lacking for dichellesthiiiforms, with only one complete life cycle being known (Cabral, 1983). The discovery of a dichellesthiiiform frontal organ or frontal filament would require re-evaluation of the phyletic position of its owner's family.

Within the dichellesthiiiform assemblage parallelism and convergence are thought to be common, especially as they concern trends in body tagmosis in which thoracic segments are incorporated into the genital complex, and the reduction of the thoracic legs (see Kabata, 1979). Among dichellesthiiiforms, shared primitive characteristics are also thought to be common, mainly involving the general shape of the body (subcircular in cross section), and the structure of the cephalothoracic appendages (see Kabata, 1979; Ho, 1987; Cressey and Boxshall, 1989). Certainly the comparison of the fossil Kabatarina to other dichellesthiiiforms strengthens these ideas (see Cressey and Boxshall, 1989). However, as the only fossil copepod, K. pattersoni unfortunately is somewhat of a red herring regarding its ability to help define interfamilial relationships. Because of the above and the fact that a strong synapomorphy defining the entire assemblage is unknown, Kabata (1979) independently considered these families.

Based on the superficial morphology of some dichellesthiiiform species (i.e. general habitus and structure of thoracic legs), Hatschekiidae and Pseudocycnidae might be interpreted as primitive and closely allied. In fact, the general habitus of some hatschekiids and pseudocycnids is quite similar to that of kroyeriids, and characteristics such as the cuticular flaps and spines on the legs of some hatschekiids seem to further suggest some loose
affiliation with eudactylinids. Using similar criteria, a more derived alliance between Hyponeoidae, Lernanthropidae, and Dichelethiidae, might be considered. Such observations would structure the dichelestiiform assemblage so that Hatschekiidae and Pseudocycnidae appear primitive while Hyponeoidae, Lernanthropidae, and Dichelethiidae would seem relatively derived. Ecologically this pattern would suggest a shift from relatively more mobile to more sessile forms. However, this scheme cannot be considered robust because its promotion requires the use of many ad hoc conventions.

Pennellidae is separated from taxa further below on the cladogram and united with caligiforms and lernaeopodiforms based on the two previously mentioned characters 12 and 13 (Table 1 and Fig. 21). It should be noted that character 12 (possession of a frontal organ and use of a frontal filament during larval development) is a complex character. Although this character has not been weighted on the cladogram, further examination would probably substantiate its division into several distinct yet related characters.

The general similarity of the overall body segmentation of adult male and untransformed adult female pennellids with adults of both Dissonidae and especially Kroyeriidae are notable sympleisiomorphies. Even more striking is the similarity between the overall habitus of the mesoparasitic kroyeriid Kroyeria caseyi (see Benz and Deets, 1986) and partially transformed pennellid females (e.g. see Kabata, 1979: Figs 1342 and 1416). The convergence of these forms seems based on both a combination of plesiomorphic traits and superficial similarities associated with a mesoparasitic lifestyle. As mentioned above, pennellids also share with kroyeriids chelate second antennae (character 6 of Table 1 and Fig. 21). This character is considered homoplasious, a determination that is further supported if character 12 was reconsidered as discussed above. Lastly, pennellid females, hatschekiid males and females, and tanyleurids lack maxillipeds. This absence is
considered a loss of this appendage and is shared between these taxa through homoplasy (character 9 of Table 1 and Fig. 21).

Concerning the relationship of Pennellidae to the caligiform and lernaeopodiform lineages, the pennellid chalimus appears much like that of caligiforms. However, this form appears relatively underived based on the general segmentation of its body and appendages and, therefore, must be considered plesiomorphic and incapable of resolving affinities.

The lernaeopodiform lineage is united by four characters (see Fig. 21). The first is the possession of second antennae with prominent exopods. As discussed above, this characteristic appears to be a reversal, and is similarly shared with some siphonostomes associated with invertebrates (see character 2 of Table 1 and Fig. 21).

The second character uniting lernaeopodiforms is the possession of multiseriate egg arrangement (character 15 of Table 1 and Fig. 21). This trait is shared with the siphonostome associates of invertebrates and most likely represents a distinct character state from an evolutionary perspective. This conclusion is based on the observations that within Eudactylinidae, *Jusheyyus* has seemingly reverted to a multiseriate egg arrangement, and that within Lernaeopodidae, *Clavellistes lampri* (Scott and Scott, 1913) apparently represents a switch from a multiseriate to a uniseriate egg arrangement (see Kabata, 1979; Deets and Benz, 1987; Deets and Ho, 1988).

The third character uniting lernaeopodiforms is that all thoracic legs are modified into vestigial structures or are completely lost (character 16 of Table 1 and Fig. 21). The homoplastic relationship of this character to the reduction of the highly modified fourth legs of dichelesthiiiform members has been discussed above.
The most notable character unifying the lernaeopodiform lineage is the possession of a highly modified grub-like male and untransformed adult female (character 17 of Table 1 and Fig. 21). This character is a powerful synapomorphy which has not been weighted on the cladogram, but which could be divided into several distinct yet related characters.

Families Lernaeopodidae, Naobranchiidae, and Tanypleuridae are united and separated from Sphyriidae based on the second maxillae being highly modified and serving as the primary attachment appendages of the fully transformed adult female (character 18 of Table 1 and Fig. 21). Although transformed female sphyriids are mesoparasitic, it is interesting to note the long second maxillae of Norkus (see Dojiri and Deets, 1988) which give the impression that lernaeopodiforms may have been ancestrally united by expansive female second maxillae or the genetic ability to develop them.

Relationships among Lernaeopodidae, Naobranchiidae, and Tanypleuridae appear unresolved (see Fig. 21). Based on the work of Kabata (1966b, 1979, 1981; Kabata and Cousens, 1972), phylogenetic relationships within Lernaeopodidae depict this large family to be composed of five lineages (salmincolaforms, lernaeopodaforms, brachiellaforms, charopiniforms, and clavellaforms). The morphological diversity of transformed female lernaeopodids along with the lack of thorough descriptions of the systematically important adult males renders lernaeopodid phylogeny a difficult hypothesis to construct (e.g. see Kabata, 1979, 1990; Ho and Do, 1984). The inclusion of Naobranchiidae and Tanypleuridae into this conundrum further complicates matters.

Kabata (1979) reviewed the history of Naobranchia from its inclusion by Wilson (1915) in Lernaeopodidae (subfamily Clavellinae) to its transfer by Yamaguti (1939) as sole member of Naobranchiidae. Given current theory of Lernaeopodidae phylogeny, Naobranchia does not appear to exhibit any derived characteristics warranting independent familial status (Fig.
As recently noted by Kabata (1992) *Naobranchia* displays three basic types of males. Two types seem quite similar to lernaeopodid males, and possibly indicate parallel evolution between the males of these two families. The typical adult female *Naobranchia* first antennae seem easily acceptable as reduced lernaeopodiform antennae. The long *Naobranchia* cephalocollum is clavellaform. The distinctive band-like *Naobranchia* second maxillae which fuse with the thorax without hint of a bulla (character 20 of Table 1 and Fig. 21), appear too easily derived from within Lernaeopodidae to endorse distinct familial status. Lastly, the unusual brood sacs of some naobranchiids seem easily derived from some lernaeopodid ancestor. To support this, the brachiellaform lernaeopodid *Cryptova* Kabata, 1992 is noted as possessing brood chambers (see Kabata, 1992). Therefore, it appears that *Naobranchia* can be accommodated in Lernaeopodidae as a close relative of clavellaforms or brachiellaforms, and future studies should consider more thoroughly the suppression of Naobranchiidae.

Tanypleuridae, erected by Kabata (1969b) to hold *Tanypleurus alcicornis* Steenstrup and Lütken, 1861, likewise, seems closely related to Lernaeopodidae. Steenstrup and Lütken (1861) recognized similarity between *Tanypleurus*, *Lernaeopoda* Blainville, 1822, and *Anchorella* Cuvier, 1830 (=Clavella) in that these genera all use the second maxillae as principal attachment organs. Although Wilson (1920) also noted possible affinities between *Tanypleurus* and Lernaeopodidae, through misfortune *Tanypleurus* eventually came to reside within the poecilostomatoid family Chondracanthidae (see Kabata, 1969b). In redescribing *Tanypleurus*, Kabata (1969b) reaffirmed siphonostome status for the genus and noted its affinity with Lernaeopodidae and Naobranchiidae. In particular, Kabata (1969b) compared the dendritic holdfast of *Dendrapta* (Lernaeopodidae) with that of *Tanypleurus*. However, based on the structure of both the second antennae and first maxillae, and on the lack of maxillipeds, Kabata (1969b) erected Tanypleuridae to accommodate the species.
Considering this matter the present author notices that as illustrated by Kabata (1969b) the uniramous second antenna of *Tanypleurus* possibly represents the endopod remnant of a typical Lernaeopodidae structure. To support this possibility, *Clavella stellata* (Krøyer, 1838) is noted as having an almost uniramous second antenna composed mainly of endopod (see Kabata, 1979). Kabata (1969b) stated that the first maxilla of *Tanypleurus* resembled that of Lernaeoceridae more than that of Lernaeopodidae. The present author, however, contends that the *Tanypleurus* first maxilla as illustrated by Kabata (1969b) represents the endopod remnants of a lernaeopodid structure. To legitimize this claim it can be noted that terminal setae present on the endopods of the first maxillae of Lernaeopodidae typically are naked cylindrical papilliform setae which taper abruptly at some point along their lengths (see Kabata, 1979). Setae of the *Tanypleurus* first maxilla illustrated and described by Kabata (1969b) exhibit this form, however, those of Pennellidae (=Lernaeoceridae) do not (see Kabata, 1979). Further supporting this argument, there appears to be a tendency within Lernaeopodidae for reduction of the first maxilla into a uniramous condition displaying mainly an endopod with two lernaeopodid-type setae (e.g. see Kabata, 1979). Kabata's (1969b) mention of *Tanypleurus* lacking maxillipeds certainly denotes a regressive condition (shared with hatschekiids and pennellid females) and does not warrant independent familial status. In fact, within Lernaeopodidae at least one genus, *Tracheliastes* Nordmann, 1832, exhibits vestigial maxillipeds. In light of the above and giving special consideration to similarity between the holdfasts of *Tanypleurus* and *Dendranta* as noted by Kabata (1969b), the present author feels that it will take the discovery of a truly atypical lernaeopodid male for *Tanypleurus* to maintain familial status outside of Lernaeopodidae.

As discussed above, caligiforms share with pennellids and lernaeopodiforms a frontal organ which produces a frontal filament used during development (character 12 of Table 1 and Fig. 21), and a marked reduction in the segmentation of the first antennae (character 13 of Table 1 and Fig. 21). Although a frontal filament has not yet been observed in three
caligiform families, either it or a frontal organ has been seen in all six families (e.g. Caligidae (see Kabata, 1974b, 1981; Cressey and Cressey, 1979), Euryphoridae (see Benz et al., 1992), Trebiidae (Benz, unpublished observations), Cecropidae, (see Grabda, 1973), Pandaridae (Fig. 23; also see Benz and Last, in review), and Dissonidae (Benz, unpublished observations). The caligiform lineage, therefore, is tentatively considered to primitively possess a frontal filament based on the existence of a frontal organ as evidence of its presence (see Anstensrud, 1990b; Piasecki and MacKinnon, 1993). While the frontal filament of some caligiforms is hard to detect and may easily be overlooked, it is possible that different ecological constraints may have altered its form or presence within this lineage.

Caligiforms are united by three characters which all represent modifications of the cephalothorax. The first of these is the possession of a relatively large cephalothorax (minimally containing the first pair of thoracic legs) which is dorsoventrally flattened and whose ventral surface is concave (character 21 of Table 1 and Fig. 21). This distinctive cephalothorax, known as the dorsal or cephalothoracic shield, is primitively divided into anterior and lateral regions by cuticular thickenings not necessarily associated with the demarcation of true body segments (Parker et al., 1968; Boxshall, 1974a; Kabata, 1979). Although this shield is well-developed in caligiforms, some siphonostome associates of invertebrates possess cephalothoraxes that appear somewhat similarly flattened, although less pronounced and lacking well-defined lateral regions (e.g. Dirivultus Humes and Dojiri, 1980).

The second character unifying the caligiform lineage is the possession of two thin cuticular flaps, known as frontal plates, attached one on each side of the midline along the anterior aspect of the dorsal shield (character 22 of Table 1 and Fig. 21). Frontal plates are not seen on siphonostomes other than caligiforms.
The third character unifying caligiforms is the possession of a unique type of first maxilla which primitively is biramous, with a relatively large denticiform endopod and a small exopod apically bearing three small spiniform setae (character 23 of Table 1 and Fig. 21).

Four structures (sternal projections, postantennary processes, postoral processes, and elytra) which are widely but not universally found among caligiforms were not included in the phylogeny because their exact relationships to one another are ill-defined. Nonetheless, a brief discussion of each will serve to summarize current understanding of these potentially synapomorphic features.

Various types of sternal projections are possessed by caligiforms. The most familiar of these is the sternal furca of some trebiids, euryphoriids, and caligids (see Kabata, 1979). The sternal furca is a posteroventrally aimed medial projection between the maxillipeds and first thoracic legs which may be flexible or immovable (Fig. 24. As noted by Kabata (1981), the necessity of this furca is open to debate, as it is not universally possessed among caligiforms, and species lacking it are not noticeably affected by its absence. Several authors have suggested that application of the furca to the host substrate may provide a brake against the typical forward-aft water flow continually pressuring many caligiforms (Wilson, 1905; Gnanamuthu, 1948; Lewis, 1966b; Kabata and Hewitt, 1971).

Lewis (1966b) argued that the sternal furca possibly represents either a remnant of stylet bearing interpodal bars (as seen in Kroveria: Kroyeriidae) or stylet issuing interpedigerous plates (as in seen male Nesippus borealis (Steenstrup and Lütken, 1861): Pandaridae). In either instance the furca furnishing plate appears to have been associated with the maxillipeds. Systematic rearrangement since Lewis’s (1966b) report makes the idea that Kroveria possesses a possible precursor of this furca even more interesting. Also interesting is Lewis's (1966b) observation that male Paeon (Sphyriidae) possess second maxillae and
maxillipeds which are paired along the midline in an unclear manner relative to the form of sternal projections. As further noted by Lewis (1966b) the medial sternal stylet of the pandarid *Demoleus heptapus* (Otto, 1821) bears striking resemblance to the sternal furcae of trebiids, euryphorids, and caligids (Fig. 24). Kabata (1965, 1966a) has provided description of both a sternal furca and sternal stylet in *Dissonus*. These observations leave only Cecropidae, seemingly well-embedded within the caligiform lineage, lacking at least one representative with some form of sternal projection.

The postantennary processes are paired cuticular projections shared by many caligiforms which are also of unresolved origin (see Lewis, 1969; Kabata, 1979, 1981). These projections are found ventrally on the cephalothorax posterolateral to the second antennae of some pandarids, trebiids, euryphorids, and caligids. These processes may exist as corrugated adhesion pads (e.g. *Pandarus* and *Alebion*) or as tine-like structures (e.g. *Trebius*, *Gloioptotes*, and *Caligus*). Three groups of setules are associated with the postantennary processes, and the presence of these setules is known from other caligiforms not displaying the cuticular postantennary processes (e.g. *Dissonus*).

The postoral processes are paired cuticular projections located posterolateral to the mouth tube which are shared by many caligiforms. Like the postantennary processes, the postoral processes exist as corrugated pads (e.g. *Pandarus* and *Alebion*) or as tine-like structures (e.g. *Gloioptotes*). The postoral processes represent a modified element of the first maxilla (Lewis, 1969; Kabata, 1979). Along with the postantennary processes, they serve to prop the ventral aspect of the cephalothorax against the host substrate. Generally, species which reside on the placoid scales of elasmobranchs have a greater tendency to possess processes with corrugated surfaces while species residing on teleosts exhibit tine-like projections.
Many caligiforms also possess dorsal, ventral, and/or lateral elytra (often referred to as plates). While some pandarids possess plate-like structures associated with the abdomen, most caligiform elytra are associated with the thoracic segments. These outgrowths exhibit bilateral symmetry and are sometimes fused along the midline to form a single shield (e.g. plates associated with the third and fourth pedigerous segments of Pandarus species). Kabata (1979) considered the caligid dorsal shield to be partially formed by the fusion of several such plates. Comparison of the dorsal shield of dissonids, pandarids, cecropids, trebiids, euryphorids, and caligids (e.g. cf. Kabata, 1966a; Benz and Deets, 1987, 1988; Benz, 1989; Deets and Benz, 1988; and Deets and Dojiri, 1989) supports Kabata’s (1979) premise, as it appears that the posterior sinus of trebiids, euryphorids, and caligids is laterally bound by the remnant of a lateral plate associated with the second pedigerous segment, whereas in dissonids, pandarids, and cecropids the posterior sinus is not as well-delimited and is laterally bound by pre-second pedigerous segment components. Although lateral plates associated with the posterior sinus are known to assist in attachment by sealing the dorsal shield, the functions of other cuticular alae are generally unknown. Kabata (1979) noted that female Anthosoma crassum (Dichelesthiidae) possess elytra which seem to offer protection from encroaching host tissues. However, unlike Anthosoma, caligiforms seldom are deeply embedded in their hosts. The ventral surface of some lateral plates of pandarids possess a corrugated surface which may (e.g. Pandarus species) or may not (e.g. Nesippus species) be expanded into an adhesion pad. Corrugated surfaces would seem to assist in attachment by functioning as friction plates. Elytra are added throughout development from copepodid to adult, and other than those seemingly associated with locomotion and attachment, the alae of male caligiforms are typically fewer and/or smaller than those of their corresponding females.

Kabata (1979) proposed that the caligiform lineage was composed of two groups, the first lacking dorsal and lateral plates (considered represented by Dissonidae, Trebiidae, and
Caligidae), and the second possessing such plates (considered represented by Pandaridae, Cecropidae, and Euryphoridae). Within each group Kabata (1979) hypothesized an evolutionary trend involving a step-wise process of cephalization incorporating the natatory thoracic segments into the cephalothorax. Although this process is quite evident among caligiforms, Kabata's (1979) two group proposal must be questioned because as noted by Dojiri (1983) the presence or absence of dorsal and lateral plates does not so conveniently cleave caligiforms into two groups.

Dojiri's (1983) consideration of interfamilial relationships among caligiforms regarded the group to be composed of two clades. One consisted of Pandaridae and Cecropidae, and the other of Dissonidae, Trebiidae, and Caligidae (into which Dojiri placed Euryphoridae). To this author, the characters used by Dojiri (1983) to support two caligiform clades seem unconvincing and/or ill-defined. For example, the long and slender mouth tube that Dojiri (1983) assigned to the pandarid-cecropid clade seems to be a very graded characteristic which appears related to the functional constraint of having to feed between the raised placoid scales of elasmobranch hosts (see Fig. 22). The dentiform process which distinguishes Dojiri's (1983) dissonid-trebiid-caligid clade is only slightly modified among pandarids and cecropids. The possession of biramous legs one-four that distinguishes Dojiri's (1983) pandarid-cecropid clade is a characteristic shared with dissonids. Lastly, the trend toward reduction of the segmentation of legs one-four in Dojiri's (1983) pandarid-cecropid clade is a character which probably represents a homoplasy, having happened on several occasions within the caligiform lineage. Support for this argument comes from a similar general trend within Dojiri's (1983) dissonid-trebiid-caligid clade.

Based on the present analysis there appears no justification to split the caligiform lineage into two clades (see Table 1 and Fig. 21), and yet the herein proposed phylogeny depicts the evolution of cephalization among caligiforms as generally proposed by Kabata (1979) and
Dojiri (1983). Although this author feels inclined that Dissonidae represents the most primitive caligiform family (a premise more boldly advanced by both Kabata, 1981 and Dojiri, 1983), strong character evidence supporting this remains unfound. The idea that dissonids are most primitive appears to be linked to the overall appearance of their habitus, a form that appears unspecialized and in which sexual dimorphism is unpronounced. While this form contrasts sharply with cecropids and modified pandarids, it does not conflict greatly with unmodified pandarids such as *Pagina* and *Demoleus* Heller, 1865. This phylogenetic analysis, therefore, considers Dissonidae to be the sister group to a clade consisting of Pandaridae and Cecropidae (see Fig. 21). The pandarid-cecropid clade is marginally set apart by possessing first maxillae with relatively small rami and endopods not distinctly dentiform (character 24 of Table 1 and Fig. 21).

While Pandaridae and Cecropidae appear closely allied, their separation has historically been problematic. Kabata (1979) proposed that the shape of the female corpus maxillipedis (squat with myxal region displaced distally in Pandaridae, slender in Cecropidae) can be used to distinguish these two closely related families (see character 25 of Table 1 and Fig. 21). A recent redescriptions (Benz and Deets, 1988) of the cecropid *Entepherus laminipes* Bere, 1936 has strengthened Kabata's (1979) criterion. In addition to the maxillipeds of *Entepherus* fitting the cecropid form, the report of Benz and Deets (1988) is important because it offers evidence that the dissimilarity displayed between the maxillipeds of pandarids and cecropids is not due to functional constraints. This conclusion is made because *Entepherus* is the only cecropid which is parasitic on elasmobranchs, and prior to a detailed description of its maxillipeds one might have considered that differences in host substrates (i.e. surfaces with placoid scales versus surfaces without them) rather than common ancestry may have determined the different maxillipeds of pandarids and cecropids. Adding further evidence that this difference between pandarids and cecropids is free from functional bias, it should be noted that among pandarids (all of which are parasitic on
elasmobranchs) squat maxillipeds with their myxal regions displaced distally are found on both species which attach to surfaces with and without placoid scales (cf. Figs 15 and 25). Comparisons among the maxillipeds of dissonids, pandarids, and cecropids suggest the form shared by pandarids to be derived.

Continuing up the caligiform clade, Trebiidae is separated from Dissonidae and the pandarid-cecropid clade by possessing a cephalothorax into which the first and second thoracic legs have been incorporated (character 26 of Table 1 and Fig. 21). Trebiidae also shares with Euryphoridae and Caligidae first maxillae which are distinctively composed of two parts (character 27 of Table 1 and Fig. 21).

Finally, in Euryphoridae and Caligidae the first three pairs of thoracic legs become incorporated into the cephalothorax (character 28 of Table 1 and Fig. 21), with the third pair and their interpodal bar forming a posterior seal for the cephalothorax (character 29 of Table 1 and Fig. 21). All euryphorids and caligids except Euryphorus (Euryphoridae) also share the apomorphy of possessing uniramous fourth thoracic legs (character 30 of Table 1 and Fig. 21). This author must concur with Dojiri (1983) that Euryphoridae and Caligidae currently seem impossible to differentiate from one another.

EVOLUTIONARY BIOLOGY OF SIPHONOSTOMES PARASITIC ON VERTEBRATES

Historical considerations can provide rich insight. For biologists, Darwin legitimized this endeavor by viewing biological process in an evolutionary context. Since Darwin, the who, what, where, and when questions become answered through the reclamation of historical pattern, and the curious why questions associated with historical process are most rightfully placed in tow. Evolutionary studies of free-living organisms are difficult enough, and
similar considerations of parasitic taxa are inescapably hindered by the need for yet further layers of information.

Although many phenomena are open to evolutionary inspection, larval development, adult natural history, and host associations are of particular interest to parasitologists. In this thesis it seems appropriate to add to this list the invasion of fresh waters, as the siphonostomes infecting vertebrates have several veterans of this significant ecological transition. It also is appropriate to consider the temporal origin of the siphonostomes parasitic on vertebrates, mainly because fossils virtually do not exist for these animals and tracing origins is fascinating, but also because studies of the possible coevolution of parasites and their hosts require the assumption of equally ancient hosts and parasites.

**Trends in Larval Development**

Although our knowledge of the ontogeny of the siphonostomes parasitic on vertebrates is incomplete, data suggest that several developmental incidents and trends have punctuated the evolution of these copepods (Figs 26 and 27). A life cycle with ten stages (two nauplius, one infective copepodid, four parasitic copepodid, two preadult, and one parasitic adult stages) appears to be a primitive characteristic among the siphonostomes parasitic on vertebrates (Figs 26 and 27).

The free-living and typically motile nauplius stages disperse copepods throughout host populations. For parasitic species which must secure hosts, a tradeoff logically exists between larval dispersal and larval security. Nauplius stages are suppressed in several orders of Copepoda infecting vertebrates (Kabata, 1981; Raibaut, 1985). Among the siphonostomes parasitic on vertebrates, a reduction in the planktonic nauplius stages that presumably
reduces dispersion is seen in several taxa (Fig. 26). For example, observations of *Dissonus nudiventris* suggest that the balancers of its nauplius may be crudely used to snag its mother's ruptured egg sacs. Such entanglement would seem to ensure the subsequent copepodid stage's close proximity to a suitable host (Anderson and Rossiter, 1969). Sphyriids and some lernaeopodids and pennellids complete precopepodid development within the egg so that hatching liberates an infective copepodid (Fig. 26). This process could be viewed as a combination of delayed hatching and precocious development.

Enormous somatic development produces a copepodid from a nauplius. The first siphonostome copepodid typically exhibits a cephalothorax with five pairs of cephalothoracic appendages, a number of biramous swimming legs individually issued from the cephalothorax and free thoracic segments, and an abdomen bearing a pair of caudal rami. Among siphonostomes, the first copepodid is maintained as the primary infective stage (Fig. 26). This is a life history characteristic that is shared with Poecilostomatoida (Kabata, 1981; Raibaut, 1985). Upon securing its host the infective copepodid undergoes one to six molts which ultimately transform it into a preadult or adult (Fig. 26).

The term chalimus is often used for copepodids that tether themselves to their hosts via a frontal filament. The frontal filament is produced by the frontal organ during the infective copepodid stage, and can often be seen in its coiled and untriggered condition within the anterior portion of the cephalothorax of some copepodids. Upon securing its host, the infective copepodid extrudes the frontal filament and securely anchors it. Once fastened, the copepodid molts into what is generally considered the first parasitic stage, the first chalimus.

The frontal filament is absent in Lernanthropidae (Fig. 26) and based on similarities in general lifestyles (Fig. 27) possibly also in Eudactylinidae, Kroyeriidae, Hatschekiidae, Pseudocycnidae, Hyponeoidae, and Dichelesthiidae. The presence of the frontal filament
seems associated with an ecological shift from the branchial chamber and olfactory capsules to the general body surface (Fig. 27), as well as with the appearance of derived modes of adult attachment (see below).

The frontal filament fastens the chalimus during the molting process and provides unyielding security for young copepods that have not yet developed adult holdfast mechanisms. But, as seen in Lernanthropidae, this tether is not required by all siphonostomes parasitic on vertebrates. How these copepods stay attached to their hosts during molting is not well known, however, copepodids that tightly attach to their hosts either by burrowing or through deep penetration of the host with attachment appendages would seem capable of emerging from still anchored exuviae and re-attaching nearby. Although this has not been observed, it seems possible that some lineages never needed the frontal filament, and that other taxa may have modified or reduced their reliance on it. For example, the short thin frontal filament of *Echthrogaleus torpedinis* described by Benz and Last (in review) appears too feeble to support a larva throughout its entire development. It is possible that as some copepods molt and develop adult mechanisms of attachment the need for the frontal filament becomes solely associated with the molting process. For Caligidae it might be advantageous for early larvae to be permanently tethered to the host. Swinging on the end of their frontal filaments, these superficial grazers could forage over a relatively wide region. However, for some caligiforms which infect elasmobranchs and who insert their relatively long mouth tubes between the placoid scales of their hosts, a less wavering attachment mode might be required to allow the oral cone to remain stationary. Such an attachment mode might be facilitated by the placoid scales themselves or methods involving the invasive application of attachment appendages.

Virtually nothing is known of the energy requirements of developing siphonostome larvae, and therefore the real value of the frontal filament is unknown. However, beyond mooring
the chalimus throughout the molting process, the frontal filament presumably provides a strong passive form of attachment requiring little maintenance energy. Unknown also is what life at the end of the frontal filament is like. For example, many caligiforms and pennellids exhibit relatively short frontal filaments which ensure that the mouth tube could contact the host and allow feeding. Contrarily, many lernaeopodids possess extremely long frontal filaments (e.g. see Benz, 1991) which would offer them a larger feeding area, but which seemingly would unpredictably dangle them about unless the second antennae and/or maxillipeds were used to grasp the host.

While developmental observations are needed to settle the issue concerning which siphonostome taxa parasitic on vertebrates possess a frontal filament, comparative studies of frontal filaments are also needed. This is because preliminary observations (albeit sketchy) indicate possible structural differences among the frontal filaments of siphonostomes that may denote homologous relationships or analogous representations of obvious evolutionary significance. Careful comparisons are also needed with nicothooid frontal filaments (see below) to fully understand the phylogenetic implications of this ecologically useful structure.

Just prior to adulthood up to two preadult stages may exist (Fig. 26). Kabata (1981) stated that the preadult stages represent that period when the copepod either settles definitely on its host and undergoes metamorphosis, or otherwise attains its final level of organization without aid of the semi-permanent protective larval attachment. In discussing the preadult stage in Ergasilidae (Poecilostomatoida), Kabata (1981) further stated that the difference between the copepodid and preadult could be more semantic than substantial. Kabata's (1981) remarks are valid because in some instances no solid characteristic delineates so-called preadult stages from the earlier larval series while in the rest of all instances nothing delimits them from actual adults. It is not surprising, therefore, that some authors have not
used the term preadult, instead opting to classify these stages as copepodid, chalimus or adult (e.g. see Lewis, 1963).

A general shortening of the later larval series is exhibited by Pennellidae and Lernaeopodidae (Fig. 26), and based on the similarities among lernaeopodiforms a similar trend is probably also present in Sphyriidae, Naobranchiidae, and Tanyleuridae. In Pennellidae and Lernaeopodidae a discrete preadult stage does not occur. After the last chalimus stage the untransformed adult female metamorphoses without molt into her final habitus. Males, likewise, become functional adults after the last chalimus. The greatest reduction of the larval series is seen in some lernaeopodids (Fig. 26) that display only three life history stages (i.e. one nauplius, one copepodid, and the pupa-adult). The highly motile Caligidae have retained all ten life history stages (Fig. 26). This fact raises the question of whether or not the relatively complex organization of these copepods dictates maintaining the entire developmental series. It is also notable (Fig. 26) that the greatest tendency toward a reduction of larval stages among the siphonostomes parasitic on vertebrates appears shared by lineages such as Pennellidae and Lernaeopodidae (and presumably other lernaeopodiforms as well) that possess the most highly transformed adult females. Certainly, however, the forms of the retained chalimus stages of Pennellidae and Lernaeopodidae are quite different. Pennellids maintain a rather primitive, highly motile, and streamlined appearance while lernaeopodids appear as grub-like pupae. The two host life histories of pennellids possibly place selective pressure on the untransformed adults (mainly the females) to retain a form capable of swimming, because it is this stage which must actively seek the definitive host.
Siphonostomes infecting vertebrates display a general trend in adult sexual dimorphism manifested as a relatively smaller adult male (Fig. 1) often with better developed sensory and locomotory setae than its mate (see above). These male characteristics are generally considered primitive traits (Kabata, 1979), and prompt appraisal of the often regressive appearance of the adult female as a derived product of evolution. The male accrues its adult characteristics sequentially throughout ontogeny and upon reaching adulthood continues to undergo only slight changes in appearance associated with general somatic growth. At the stage of young adulthood the sensory and locomotory armature of the female is less well-developed than those of the male, though the general habitus might not be extremely dissimilar. However, soon after firmly attaching to her host, and often subsequent to copulation, the female proceeds to grow without molt into a form that can range from mildly enlarged and retaining the general male configuration to forms so bizarre that the process is best envisaged as a metamorphosis (Fig. 26; also see above).

Species within Eudactylinidae, Kroyeriidae, Hatschekiidae, Pseudocycnidae, Hyponeidae, Lernanthropidae, and Dichelestitidae exhibit sexual dimorphism that usually is not very pronounced (e.g. see Fig. 1A-C). Among these copepods, males and females of any one species usually have similar ecological traits (i.e. sessile, semi-sessile, or errant). Kroveria caseyi is a striking exception to this generality in that it possess typical males and mesoparasitic adult females. Although its males are undiscovered, Carnifossorius siamensis Deets and Ho, 1988 is probably similarly sexually dimorphic. It is notable that the same mechanisms used to secure males to their hosts are also used to grasp females during copulation in the above mentioned families (e.g. see Benz and Adamson, 1990). While this illustrates the versatility of the holdfast appendages, it also indicates that there is at least
some minimal similarity in shape between the host substrate and portions of the female which males seek to grasp.

Members of Pennellidae routinely develop extremes of adult sexual dimorphism (Fig. 1D). The adult male and untransformed adult female are only mildly dissimilar, and each exhibits an active ectoparasitic lifestyle. However, after copulation and upon attaching to the definitive host the female assumes a mesoparasitic lifestyle accompanied by a sizable metamorphosis.

Caligiforms exhibit three general types of sexual dimorphism. The first is exemplified by Dissonidae, Trebiidae, and many members of Euryphoridae and Caligidae and consists of highly mobile adults of both sexes. Males differ mainly in being smaller and retaining slightly more elaborate sensory and locomotory setae as well as in modifications of the maxillipeds and second antennae (Fig. 1E). The second antennae are used during copulation in Caligidae (Anstensrud, 1990b), and their modification in highly active males may have been facilitated by the ability of the cephalothorax to provide succoral attachment in more derived caligiform taxa (e.g. Trebiidae, Euryphoridae, and Caligidae). The second type of caligiform sexual dimorphism is exemplified by many members of Pandaridae and some members of Euryphoridae and Caligidae and consists of the above described adult male paired with a relatively sessile adult female (Fig. 1F). Certainly this is the most dissimilar caligiform pairing, as the ovigerous female typically is heavyset and sometimes possesses a cephalothorax that lacks the marginal membrane. The third type of sexual dimorphism among caligiforms is exemplified by many Cecropidae members and consists of relatively sessile adult males and females (Fig. 1G). Typically, these males retain a smaller size and more elaborate sensory and locomotory setae than their respective mates, however, relative to other caligiform males they are quite large and are capable only of limited crawling movements.
Lernaeopodiforms show two types of sexual dimorphism. The first is seen in Sphyriidae and consists of pupaform adult males and young adult females, and relatively large, transformed mesoparasitic females (Fig. 1H). The second type is displayed by members of Lernaeopodidae and Naobranchiidae (and presumably Tanyleuridae also) and consists of pupaform adult males and young adult females, and relatively large, permanently attached, transformed ectoparasitic females (Fig. 1I).

When adult ecological characters of the siphonostomes parasitic on vertebrates are mapped onto the phylogeny of familial relationships it appears that mesoparasitism has independently evolved several times (Fig. 27). Studies of Eudactylinidae (Fig. 2; also Deets and Ho, 1988), Kroyeriidae (see Benz and Deets, 1986; Deets, 1987), and Pennellidae (Fig. 10; also Boxshall, 1986) indicate that once mesoparasitism is firmly established within a lineage a return to ectoparasitism is unlikely. Given the modifications exhibited by mesoparasitic females, explanations of this phenomenon involving natural selection seem obvious. However, there appears no logical reason why a lineage could not return to an ectoparasitic lifestyle via either the modification of the adult metamorphic program or via the processes of neoteny or progenesis. However, generally we must consider that mesoparasitic siphonostome lineages appear directed toward deeper associations with their hosts, and that the presence of a nauplius and/or copepodid stage which must be shed into the environment may represent the barrier precluding true endoparasitism. Of course this indicates an ectoparasitic origin for siphonostomes parasitizing vertebrates, a conclusion also supported by data from studies of the relatively primitive families Eudactylinidae and Kroyeriidae (see Benz and Deets, 1986; Deets, 1987; Deets and Ho, 1988). Kabata (1982) commented that the burrowing habits of many siphonostome larvae may have ultimately been responsible for or facilitated the evolution of mesoparasitic lineages. However, no matter what its origin, mesoparasitism appears to have been one method allowing siphonostomes to affix
themselves about the general body surface of active fishes. It is notable that this firmest method of attachment has produced adult females that are dramatically larger than their ectoparasitic relatives and conspecific mates. It is further important that this increase in size has been realized through a number of developmental schemes involving different somatic regions. For example, in Carnifossorius the bulk of the embedded body represents the first pedigerous segment, while in pennellids, sphyriids, and Kroveria caseyi this portion represents the thoracic segments and some of the genital complex.

Caligiforms are evolutionarily interesting because they represent a very successful lineage which often is associated with the general body surface of their hosts. Unlike pennellids and lernaeopodiforms, caligiforms have not evolved widespread provision for permanent passive attachment. Instead they have evolved two basic lifestyles. Pandaridae and Cecropidae seem to have followed a trend toward increasing the sessile nature of the adult female. Dissonidae, Trebiidae, Euryphoridae, and Caligidae appear to have maintained and/or exploited a more mobile existence. As if dictated by necessity, the swimming legs seen within these more active families appear more conservative than those possessed by more sessile pandarids and cecropids. While the evolution of these differences is hard to explain, the placoid scales which typically cover elasmobranchs appear to offer a very stable substrate on which to permanently attach (see Benz, 1992), and which might somewhat release the thoracic legs from functional use. On the other hand, the relatively smooth and seemingly hard to grasp body surface of teleosts should encourage the evolution of mechanisms enhancing the ability to rapidly attach. Such mechanisms naturally would involve both powerful swimming and efficient settling abilities as seen in most caligids. However, the common existence of fast swimming pandarid males of considerable size on many species of elasmobranchs indicates that a sessile lifestyle need not be a prerequisite for caligiforms infecting elasmobranchs, and as mentioned above some caligid females are relatively sessile as adults (see Fig. 20).
Routine attachment at particular locations on the host is a parasitic phenomenon often exhibited by siphonostomes that infect vertebrates, and generally speaking, these parasites have quite successfully invaded the external surfaces of fishes (Table 2). The relatively random initial distributions of larvae (e.g. see Kabata and Cousens, 1977; Anstensrud and Schram, 1988; Benz, 1989) reveal that site selectivity often intensifies throughout life, and further suggests that the phenomenon of site specificity may be related to maturation and reproduction. The relatively random distribution of larvae and nonrandom distribution of adult females also suggests that highly efficient mechanisms of autoinfection (i.e. the host being infected by the progeny of parasites residing on it) are not well-developed because if they were one would expect the distribution of infective larvae to better resemble the distribution of ovigerous females. Males representing several different familial lineages have been noted to exhibit wider distributions than females (Benz, 1980; Benz, 1986; Benz and Dupre, 1987; Anstensrud, 1990c). Benz and Dupre (1987) proposed that water flow about the gills of blue sharks was responsible for the initial distributions of Kroeyeria carchariae MLAuci, and that males ranged over a wider area in search of mates throughout the ranks of gill filaments. Other distributions are more difficult to explain. For example, many adult female caligidorms are found in dense clusters attached at very restricted and predictable locations on their hosts (Figs 18 and 20; also see Benz, 1980; Anstensrud, 1990c). A convincing explanation for these distributions is lacking. Benz (1980) noted that Pandarus satyrus Dana, 1852 individuals which appeared to assume more posterior positions in clusters seemed to be younger adult females and that males tended to associate most with these peripheral females. Anstensrud (1990c), however, noted in observing Lepeophtheirus pectoralis that most copulatory activity took place away from clusters and that males seldom frequented them.
Several siphonostome lineages infect both the branchial chambers and olfactory capsules of their vertebrate hosts (Fig. 27). The branchial chambers of fishes offer small parasites an orderly yet heterogeneous environment best envisaged as consisting of many niches (Figs 6 and 8). Within the branchial chambers, most members of Eudactylinidae, Kroyeriidae, Hatschekiidae, Pseudocycnidae, Hyponeoidae, Lernanthropidae, and Dichelesthiidae tend to be intimately associated with the gill filaments of their hosts (Wilson, 1932; Kabata, 1979; Benz, 1980; Davey, 1980; Benz and Dupre, 1987; Benz and Adamson, 1990). Although a few caligiforms attach directly to the gill filaments, most residing in the branchial chamber are associated with the interbranchial septa of elasmobranchs or the gill arches. Pennellids and sphyriids infecting the branchial chambers are likewise distributed, although the crypting these relatively large sessile copepods cause on the gills can affect large regions of the respiratory surface (see Grabda, 1991). As discussed above, naobranchiids are confined to regions of the gills where they can encircle a gill filament with their second maxillae. Lernaeopodids and tanypleurids require an attachment substrate which will support the female anchoring system, and within the branchial chambers the interbranchial septa and tissues capping the efferent arterioles of elasmobranchs, the tissues capping the afferent and efferent arterioles of teleosts, the gill arches, and the branchial chamber walls best provide this requisite.

The gills and olfactory capsules of elasmobranchs show many similarities (Fig. 28), and siphonostomes infecting olfactory capsules tend to occupy niches similar to their close relatives residing within the branchial chambers (Fig. 28). In presenting an ecological summary of Kroyeriidae, Deets (1987) noted the probable habitat shift of some proto-kroyeriid from the branchial chamber to the olfactory capsule of chondrichthyans. In light of the similar construction of the olfactory capsules and gills of these primitive fishes (Benz, 1984, in preparation), such a habitat shift raises an interesting question. Have some siphonostomes invaded the olfactory capsules of fishes from the branchial chambers because
these habitats represent analogous and ecologically conservative environments, or are the olfactory capsules modified branchial chambers which through their derivation from the gills provided a powerful vicariant event that promoted the isolation and subsequent speciation of parasite inhabitants?

Several authors have speculated on the possibility that the olfactory capsules were derived from premandibular gill pouches (see Dohrn, 1875; Marshall, 1881) or gill arches (see Bjerring, 1972, 1973; Bertmar, 1972). Unfortunately, the developmental programs that result in forming the olfactory capsules of extant fishes appear so derived that compelling evidence linking the origin of the olfactory sacs to the gills may no longer exist (see Jollie, 1977). While the present author would not challenge that original innovations can arise independently within the framework of evolution, he would also argue that in considering the origin of the olfactory capsules, parsimony would seem to favor derivation of these rather complicated structures from the similarly organized gills (see Fig. 28). Such pathway seems even more likely given the serial nature of the gills and the universally accepted theory that a similar process involving the modification of gill arches led to the formation of true chordate jaws. If evolution of the olfactory capsules was immediately instrumental in isolating siphonostome lineages such as *Kroeyerina*, it would mark the presence of vertebrate infecting siphonostomes at least as far back as the Ordovician (441-504 mya) and would extend the association between siphonostomes and chordates to include some (if not all) of the earliest vertebrates (Stahl, 1985; Chaline 1990).

The ecological shift from the branchial chambers and olfactory capsules to the general body surface was apparently coincident with the appearance of the frontal filament (Fig. 27) and might have been further facilitated by three different modes of extending this attachment security throughout adulthood. As discussed above, adult pennellids and sphyriids evolved mesoparasitic females capable of securing the host. Pennellidae retained a small swimming
male while Sphyriidae shares with Lernaeopodidae and Naobranchiidae (and presumably also Tanypeuridae) a crawling grub-like male. Adult female lernaeopodids, tanypeurids and some caligiforms permanently attach to their hosts via superficially invasive methods. Other caligiforms use a suctorial attachment mode which provides firm grasp yet can be vented to free these able swimmers to move about their hosts. Although shifts from the branchial chambers and olfactory capsules seem to coincide with morphological changes in both sexes, the form of the adult female appears to have been altered more radically, and these alterations are often reflected in a larger overall female size which is generally thought to be associated with increasing reproductive potential (Kabata, 1979).

Trends in Host Associations

Many siphonostomes appear particularly well-adapted and consequently appear restricted to particular hosts. For example, the unique holdfast of Naobranchiidae which must encircle a gill filament appears to confine this family to the gills of teleosts (Fig. 8). Similarly, the noninvasive method of attachment and long vermiform bodies of most Kroveria species seem tailored to living in the water channels formed by the gill filaments and interbranchial septa of chondrichthyan (Fig. 4; also see Benz and Dupre, 1987). Further still, the lock and key mode of attachment exhibited by Pandanus species certainly appears to restrict these parasites to the placoid scales of elasmobranchs (Fig. 15; also see Benz, 1992). However, even these best examples of morphologically founded host restriction seem incomplete, as respectively among teleosts, chondrichthyan, and elasmobranch, Naobranchiidae, Kroveria, and Pandanus are relatively host specific.

The radical ecological transitions exhibited within some otherwise conservative siphonostome lineages make the host specificity generally displayed by siphonostomes even
more difficult to understand. This is because these transitions suggest that as a group these parasites may be at least periodically capable of speciation involving major lifestyle alterations (e.g. see discussions above of *Kroveria caseyi* and *Carnifossorius*). Therefore, facile rationalizations of siphonostome-host associations based solely on morphological adaptation are usually inadequate to explain why these parasites have not additionally invaded seemingly available hosts and niches.

Nonetheless, as discussed above, one cannot help but notice that siphonostome infections have permeated Pisces and more remarkably have invaded Cetacea, and that some siphonostome characteristics may have preadapted or have come to adapt certain copepod species to certain hosts. For example, the relatively long mouth tubes of many *Pandarus* species allow them to feed beyond the hard nutritionally unsuitable placoid scales that cover the general body surface of many elasmobranch hosts. Similarly, the mesoparasitic lifestyle of *Pennella balaenoptera* Koren and Danielssen, 1877 seems conducive to infecting large and relatively smooth skinned cetaceans.

The ability of siphonostomes to develop efficient attachment mechanisms capable of securing highly active hosts must have been instrumental during the early colonization of fishes. As the two most successful families of siphonostomes parasitic on vertebrates, Caligidae and Lernaeopodidae have each evolved a distinct mechanism to accomplish this. For caligids, the high mobility and ability to rapidly attach to a host perhaps was one factor responsible for speciation success because it facilitated the invasion of new host taxa by highly mobile copepodids, preadults, and adults. For lernaeopodids, the evolution of a permanent method of attaching to the host along with some shortening of the life cycle seems significant.
Since at least von Ihering (1891), parasitologists have postulated that parasites may evolve along with their hosts and that congruent patterns of phylogeny between hosts and their parasites may reflect this process. For the parasitologist, often denied a meaningful share of the fossil record, such reasoning has become an imaginative time machine fueled by the phylogenetic relationships of hosts and potential former hosts.

Copepodologists have recently begun to use phylogenetic techniques such as cladistic analysis and host mapping to try and better understand the historical relationships between parasitic copepods and their hosts. To date, these types of studies of various siphonostome taxa have revealed varying degrees of phylogenetic congruence with host taxa (e.g. see Ho, 1983, 1989; Deets, 1987; Benz and Deets, 1988; Deets and Ho, 1988; Dojiri and Deets, 1988; Ho, 1992). Instances of incongruence between parasite and host phylogenies are thought to denote colonization episodes mediated more by ecology than phylogeny. Surprisingly, however, cases of strict agreement between host and parasite lineages are more difficult to assess. This is because congruent regions of host and parasite phylogenies often exhibit an enormous disparity between the phylogenetic breadth of the represented parasites and the phylogenetic breadth of the represented hosts. This disparity usually is caused by the phylogenetic scope of the host taxa present (as determined by parasite records) far exceeding that of the parasites analyzed (i.e. many host species which are members of the host groups delimited by the studied parasites have no known parasites associated with them). Without additional data, it is impossible to explain this common phenomenon. Certainly the undersampling of parasites cannot be entirely responsible for these differences. Furthermore, although explanations involving the extinction of parasites theoretically could account for such differences, such hypotheses need sound biological data to be properly advanced, and these data are seldom available.
No matter how these instances of host-parasite congruence are explained, it is interesting that to date no study examining phylogenetic congruence between siphonostomes and their hosts has determined a strict stepwise association of host and parasite species (see Deets, 1987; Benz and Deets, 1988; Deets and Ho, 1988; Dojiri and Deets, 1988; Ho, 1992). If we accept that siphonostome copepods are approximately the same evolutionary age as their hosts (and this assumption is an axiom of phylogenetic studies of the coevolution between parasites and hosts) then we must accept that generally they have exhibited a lower speciation rate or higher extinction rate than their hosts. Parasitic taxa in general exhibit this phenomenon, together suggesting that the lifestyle of parasitism is often linked to lower speciation rates than those of associated hosts. Of course some parasite taxa have apparently speciated as fast as or faster than their hosts. An example of this from among the siphonostomes parasitic on vertebrates is the cecropid clade consisting of Philorthagoriscus, Orthagoriscicola, and Cecrops, all which are virtually exclusive parasites of the ocean sunfish (Benz and Deets, 1988).

The importance of host phylogeny and history cannot be overstated when considering the evolution of parasitic lineages. Certainly the fossil record indicates that various host and potential host lineages have originated, gone extinct, or otherwise increased and decreased over time. It seems logical to assume that this biotic flux has played a major role in the evolution of parasitic lineages in a manner analogous to and layered upon the geological, geographical, and climatic changes commonly accepted as influencing the evolution of free-living lineages, and upon the more controversial catastrophic events that may have punctuated the biological record (see Raup, 1991).
Invasion of Fresh Water

Siphonostomatoida exhibits a modicum of success in fresh water, having moved into this environment at least twice (Fig. 27). One caligiform can complete its entire life cycle in fresh water. *Caligus lacustris* Steenstrup and Lütken, 1861 (Caligidae) occurs in the Baltic, Black, Azov, Caspian, and Aral Seas, and adjacent brackish waters (Grabda, 1991). Although adults are good swimmers and are sometimes found among the plankton and upon many species of fish, cyprinid fishes (Cyprinidae) seem to be preferred hosts (Yamaguti, 1963; Grabda, 1991). Adult *C. lacustris* are found on the gills and general body surface of their hosts (Markewitch, 1976), while chalimus larvae are commonly found attached to the fins (Grabda, 1991). It is very likely that *C. lacustris* evolved into a freshwater species from marine caligid ancestors, and recently Gusev and Kabata (1991) have determined that among over 200 congeners, *C. lacustris* appears most closely related to four species (*C. curtus* Müller, 1785, *C. minimus* Otto, 1821, *C. mugilis* Brian, 1935, and *C. dicentrarchi* Cabral and Raibaut, 1987) whose ranges overlap to varying degrees.

About 30 salmincolaform lernaeopodid species grouped in seven genera (*Achtheres* von Nordmann, 1832; *Basanistes* von Nordmann, 1832; *Tracheliastes* von Nordmann, 1832; *Cauloxenus* Cope, 1871; *Salmincola* Wilson, 1915; *Coregonicola* Markevich, 1936; *Pseudotracheliastes* Markevich, 1956) can only complete their life cycles in fresh water. These genera are restricted to the northern hemisphere, with a fair number of their species displaying circumpolar, Palaearctic or Nearctic distributions (Kabata, 1969c; 1979; 1988a). Host affiliations of freshwater lernaeopodids are fairly restricted, with many anadromous salmonids (Salmonidae) and sturgeons (Acipenseridae) serving as hosts. Adult females of some genera (e.g. *Salmincola*) are sometimes found in oceanic waters on anadromous fishes, however, these individuals are unable to reproduce in marine environments (Kabata, 1979).
Kabata (1979, 1981) considered salmincolaform to have invaded fresh water on some primitive salmonid during an interglacial portion of the Pleistocene (1.6-0.01 mya). Kabata (1981) also noted that because salmincolaforms are considered among the most primitive lernaeopodids such a scenario tends to compress lernaeopodid evolution into what appears a recent burst of speciation. However, Kabata (1981) reported that the study of Kabata and Ho (1981) indicated that *Neobrachiella insidiosa* (Heller, 1865) must have existed more than 50 mya (i.e. Tertiary) to be able to colonize its present distribution range. Important here is that *N. insidiosa* is a brachiellaform, a lineage of Lernaeopodidae considered far derived from ancestors of salmincolaforms (see Kabata, 1979; 1981). From these data Kabata (1981) postulated that early salmincolaforms must have existed in the marine environment long before they invaded fresh water. It is important to add to Kabata's (1981) explanation that one salmincolaform genus (*Pseudotracheliastes*) is composed of species that are exclusive parasites of sturgeons (Acipenseriformes). Sturgeons are an ancient group and could have opened fresh waters to salmincolaforms long before the arrival of salmonids, possibly as far back as 310 mya during the Pennsylvanian (see Nelson, 1976). Although no detailed phylogeny of the salmincolaform branch of Lernaeopodidae exists, Kabata (1979) noted that in some respects *Pseudotracheliastes* is more derived than *Salmincola*. However, *Pseudotracheliastes* could have evolved throughout a long relatively independent existence. Surely, a detailed phylogenetic analysis of all salmincolaform species would provide an interesting starting point for a proper discussion of how this successful lineage of Siphonostomatoida entered fresh water.

It seems logical that siphonostomes moved into fresh water under the power of their more mobile hosts rather than through self dispersal. Using this method, copepods would be ferried into freshwater environments by diadromous fishes (i.e. truly migratory fishes that move between sea water and fresh water). Although freshwater invasion could have been mediated by nondiadromous species, the relatively unpredictable nature of this mode of
access makes it seem that the rhythmic life history associated with diadromy would optimize invasion opportunity. In turn, although anadromous (i.e. diadromous fishes that migrate from sea water to fresh water to breed), catadromous (i.e. diadromous fishes that migrate from fresh water to sea water to breed), or amphidromous (i.e. diadromous fishes whose migrations between sea water and fresh water or vice versa occur regularly but not associated with breeding) fishes might serve as transport, anadromous and marine amphidromous species (i.e. amphidromous species that are born in fresh water, grow in sea water, and return to and grow and reproduce in fresh water) theoretically appear best suited for this task. This is because such species tend to be more numerous in comparison to catadromous and freshwater amphidromous species (i.e. amphidromous species that are born in sea water, grow in freshwater, and return to and grow and reproduce in sea water), and because they enter fresh water at relatively older ages and larger sizes (see McDowall, 1988) and thus would have had additional time to acquire maximum marine parasite loads. Anadromous fishes seem further desirable as agents in this process in that they often form large, dense schools as they run into fresh water to spawn (see McDowall, 1988).

Contemporary life histories of most anadromous fishes depict an existence wherein attached biota would be relatively rapidly conveyed into brackish and then fresh water. Such rapid transition into fresh water might prove too much osmotically for some external parasites. However, a more gradual transition is possible. Via this scenario copepods could reside within nearshore brackish waters on nonanadromous fishes, and upon the yearly passag of large schools of anadromous species, infective stages could attach to them. For firmly attached adult copepods (e.g. Lernaeopodidae) this would have required copepodids to be available. For motile species (e.g. Caligidae) both adults and larvae could have been involved in this host shift. In fact, today similar host shifts of sea lice (Lepeophtheirus salmonis Krøyer, 1837 and Caligus elongatus Edwards, 1840) are known to take place (Bruno and Stone, 1990).
Having reached the homestream and spawned, anadromous fishes either perish or return to the sea. Therefore, to continue thriving in fresh water, copepods (or their progeny) must locate new hosts. For motile copepod species (e.g. Caligidae) or those capable of producing infective larvae tolerant of fresh water this might be instantaneously accomplished by transferring to different host species living in the freshwater environment. On a more evolutionary timescale, persistence in fresh water may have been accomplished by maintaining association with the host as it evolved into a true freshwater species (this of course presumes a marine origin for the host species). It is interesting to consider here that natural selection could have a strong effect on parasite populations entering fresh water on iteroparous host species (i.e. species whose individuals have repetitive reproductive cycles). During the spawning migration, individual copepods which could not endure a freshwater excursion would be eliminated from the population. As postspawning fishes return to the sea, copepod veterans genetically capable of surviving the freshwater migration could produce a future generation of freshwater tolerant adults. No doubt, yearly repetition of such culling episodes would eventually result in viable populations of copepods more tolerant of fresh water. Through such a mechanism, adult copepods which permanently attach to their hosts (i.e. Lernaeopodidae, Sphyriidae, Pennellidae) might have an advantage over more motile species (e.g. Caligidae). As many know that have attempted to use osmotic imbalance to eradicate copepod infections from fishes, loosely attached individuals often dislodge themselves when they begin to become stressed. Once dislodged, these copepods are eventually doomed unless they can find another host. It might be that the survivorship in permanently attached species is a more direct reflection of osmotic tolerance in that unable to dislodge when stressed, these copepods are committed to completing the freshwater journey. The ramifications of such a selection mechanism might also immediately extend into the next generation if females were ovigerous upon entering fresh water.
A more subtle scenario accounting for freshwater siphonostomes involves an ecological inheritance mechanism. Via this method, creation of freshwater habitats from former marine environments caused by periodic changes in world sea level could have slowly allowed the evolution of freshwater copepods in situ. In reality, a similar inheritance mechanism might be linked to the evolution of diadromy in fishes and, therefore, it is difficult to consider such an inheritance scenario as being completely separate from the formerly presented invasion mechanism.

Although ovigerous females of a few parasitic copepods (e.g. *Ergasilus ilzei* Krøyer, 1863; Poecilostomatoida) have been recorded from both marine and fresh waters (see Bere, 1936; Causey, 1953; Kelly and Allison, 1962), osmotic difficulties probably represent the greatest barrier preventing marine siphonostomes from thriving in fresh water. In studying the survival of the marine species *Lepeophtheirus salmonis* held at reduced salinities, Johnson and Albright (1991b) found a direct relationship between survival rate and salinity. They proposed that these results indicated a higher energy requirement for the maintenance of a hyperosmotic state when these marine copepods are subjected to lower salinity environments.

Some disagreement exists concerning the role of osmotic pressure in the hatching of parasitic copepods (see Heegaard, 1947; Lewis, 1963; Davis, 1968). In placing ovigerous females of many marine copepod species into fresh water or unbuffered fixative, however, the present author has often been rewarded with thousands of hatched nauplii. In general, copepod larvae seem to have greater difficulty than adults with osmotic shifts (e.g. see Shields and Sperber, 1974; Johannessen, 1978; Wootten et al., 1982; Schram and Anstensrud, 1985; Johnson and Albright, 1991b). In a report to the contrary, Berger (1970; as reported in Kabata, 1981) noted nauplii of the marine caligid *Lepeophtheirus salmonis* to be more tolerant of fresh water than corresponding adults. In discussing these results Kabata
(1981) mentioned that adult L. salmonis have frequently been found on Oncorhynchus nerka (Walbaum, 1792) in British Columbia rivers far upstream in pure fresh water, but additionally stated that possibility exists that various geographic stocks of Lepeophtheirus salmonis may exhibit differences in salinity tolerance. It is notable that recently Hahnenkamp and Fyhn (1985) and Johnson and Albright (1991b) have shown Kabata's supposition to be correct in that L. salmonis from the eastern Pacific seem much more tolerant of low salinity than the same species from the eastern Atlantic.

Concerning interactions between host and parasite, Panikkar and Sproston (1941) concluded in studying the marine species Lernaeocera branchialis (L., 1758) (Pennellidae) on cod (Gadus morhua L., 1758) that mesoparasitic copepods were hyperosmotic to host blood but hypoosmotic to sea water, and that upon excision from the host copepods rapidly became isosmotic with sea water. Contrary to these findings, Sundnes (1970; as reported in Kabata, 1981) found the intestinal contents of Lernaeocera branchialis to be almost isosmotic with sea water. In studying the freshwater mesoparasitic poecilostome Lernaeac yprinacea L., 1758 on Fundulus heteroclitus (L., 1766), Shields and Sperber (1974) noted that as salinity was raised adult but not senile copepods were generally able to maintain their osmotic balance. In light of the above, Kabata (1981) seemed correct when stating that the host's role in maintaining the osmotic balance of parasitic copepods probably depends on the specific instance of host-parasite relationship and the impact of the environment on it.

At present Lernaeopodidae has no peer rival in fresh water. Current host associations suggest that lernaeopodids may have utilized large schooling iteroparous hosts to facilitate the sea to freshwater transition, and that the permanent attachment mechanism of adult female lernaeopodids may have increased the value of anadromous iteroparous fishes to their transition into true freshwater parasites through the above outlined natural selection mechanism. Additionally, the shortened life cycle of lernaeopodids, exhibiting at most one
very short nauplius stage and for some species an egg sac which directly yields infective copepodids (Fig. 26), surely seems favorable in lotic environments where pelagic dispersal of larvae becomes a risky proposition. Beyond this, the role of the bulla in mediating environmental perturbations via host-parasite exchange has not been thoroughly examined, although some studies indicate the bulla to serve some exchange purpose (Kabata and Cousens, 1972; Kabata, 1979).

By comparison, Caligidae seems to have entered fresh water via perseverance. Like lernaeopodids, caligids are well-represented on schooling iteroparous anadromous fishes, however, their life cycles typically contain at least one nauplius and two preadult stages not seen in lernaeopodids (Fig. 26). As adults caligids are also much less permanently fixed on their hosts. It is likely that the notable swimming ability of caligids during all phases of development not tethered by the frontal filament has facilitated their transfer to new hosts and environments.

It is interesting to consider why Sphyriidae and Pennellidae, whose adult females are permanently fixed to their hosts, haven't established themselves in fresh water. Sphyriids, in particular seem preadapted for this transition in that as members of the lernaeopodiform lineage they possess life cycles in which the egg sac hatches directly into an infective copepodid. However, sphyriids are a small group, half of which infect elasmobranchs, a group of fishes which has shown little evolutionary inclination to invade fresh water. The remaining half infect demersal and often deep-sea teleosts (see Yamaguti, 1963; Kabata, 1979). Pennellidae on the other hand does infect some densely schooling anadromous teleosts (see Yamaguti, 1963). However, many pennellids exploit two host life cycles, requiring the close juxtaposition of large numbers of intermediate and definitive hosts. This two host life cycle may represent a barrier to successful exploitation of freshwater habitats.
Temporal Origin of Siphonostomes Parasitic on Vertebrates

Most copepodologists would agree that if the siphonostomes parasitic on vertebrates do represent a monophyletic lineage, this lineage probably arose from siphonostomes associated with invertebrates. Unfortunately, relatively little is known about the interfamilial relationships and general life histories of the siphonostome associates of invertebrates that lends itself directly to resolving relationships with taxa parasitic on vertebrates (see Gotto, 1979). Also, it seems likely that within many siphonostome lineages evolution has followed a common parasitic pathway resulting in a reduction and loss of appendages, and this pathway ultimately muddles the issues of homology and character transformation (Kabata, 1979; Huys and Boxshall, 1991). Finally, virtually no fossil record exists for Siphonostomatoida. This makes the discussion of ancestral forms highly speculative and necessarily based on chimera-like constructions pieced together from "primitive" bits scrounged from extant taxa. Thus any consideration of the origin of the siphonostomes parasitic on vertebrates must be considered highly speculative.

Huys and Boxshall (1991) provided a detailed character set depicting an ancestral siphonostomatoid. This diagnosis is interesting in that it was primarily based on plesiomorphic characteristics displayed by siphonostomes associated with both invertebrates and vertebrates. As such it acknowledges the relatively derived state of many invertebrate associates, as well as, the seemingly very primitive characteristics of several taxa infecting vertebrates. For example, Eudactylinidae is commonly considered to represent a primitive design among siphonostomes of vertebrates (Kabata, 1976, 1981; Deets and Ho 1988; Huys and Boxshall, 1991). Some of these primitive features include highly segmented first antennae (e.g. Bariaka, Protodactylinia, male Eudactylinella alba) and a genital segment separate from the first abdominal segment (e.g. Protodactylinia). Highly segmented and seemingly plesiomorphic first antennae are also exhibited by many siphonostome associates
of invertebrates, as well as the fossil parasite of fishes Kabatarina. Notable also is that among all siphonostomes, only Protodactylina and Jusheyus (both members of Eudactylinidae) exhibit a truly separate genital somite. Certainly this must be considered a primitive characteristic for Siphonostomatoida, and its existence in otherwise primitive appearing eudactylinids parasitic on fishes leads one to consider these parasites as ancient and in some respects relictual siphonostomes. Synapomorphies that separate the siphonostomes of vertebrates from those of invertebrates notwithstanding (Table 1 and Fig. 21), the fact that Eudactylinidae and the siphonostome associates of invertebrates are set apart from other siphonostomes by having the fifth leg bearing segment free from the genital somite further attests that Eudactylinidae possibly bridges the siphonostomes of invertebrates and vertebrates (Fig. 21).

Several biogeography studies of fishes and their siphonostome parasites stake some temporal markers denoting the existence (but not origin) of various siphonostome families, for example: Lernaeopodidae 50 mya (see Kabata and Ho, 1981; Ho 1989), Lernanthropidae 110 mya (see Ho and Do, 1985), Eudactylinidae 35 mya (see Deets and Ho, 1988), and Sphyriidae over 3 mya (see Ho, 1992). The study of Eudactylinidae by Deets and Ho (1988) is particularly notable because of the generally accepted antiquity of this family (Fig. 21; also see discussion above). Deets and Ho (1988) proposed that rajiform-parasitizing eudactylinids form a monophyletic group that originated 35 mya in the Tethys Sea. This rajiform-parasitizing lineage of Eudactylinidae, however, is depicted (Deets and Ho, 1988) as a derived eudactylinid group and, therefore, its presence some 35 mya detracts nothing from the probably much more ancient origin of the family.

The only fossil parasitic copepod, Kabatarina pattersoni, provides more evidence of an ancient origin for the siphonostomes parasitic on fishes. According to Cressey and Boxshall (1989) K. pattersoni holds membership in Dichelethiidae based on one unequivocal
character. Although its familial membership in Dichelesthiidae seems tenuous, \textit{K. pattersoni} shares a number of characteristics with other closely allied families such as Eudactylinidae, Kroyeriidae, Hatschekiidae, Pseudocycnidae, Hyponeoidae, and Lernanthropidae, including the general design of its second antennae, first maxillae, and second maxillae (see Cressey and Boxshall, 1989). \textit{Kabatarina} also exhibits some very primitive characteristics. Most notably, its first antennae are composed of at least 20 segments (Cressey and Boxshall, 1989), and its maxillipeds display a distinct praecoxa and coxa (a condition unknown in siphonostomes of fishes but shared with many siphonostome associates of invertebrates (see Boxshall, 1985; Cressey and Boxshall, 1989)). In all, \textit{K. pattersoni}'s mixture of primitive and derived features suggests the probable early acquisition of fishes as hosts by Siphonostomatoida, and further attests that this transition did not necessitate the wholesale abandonment of some tried and true morphological characteristics.

Therefore, it seems that associations between siphonostomes and vertebrates must be considerably older than 110 my. But how much older? If Siphonostomatoida is monophyletic, and if its families parasitizing vertebrates likewise are monophyletic and descended from ancestors associated with invertebrates, could the first siphonostomes colonizing vertebrates have emerged with the origin of fishes during the Ordovician over 441 mya? Although highly speculative, data suggesting the evolution of the vertebrate olfactory sacs from branchial components along with some siphonostome distributions suggesting a possible shift from the gills into the nose encourage further consideration of such a history (see discussion above).

Because the phylogenetic relationships of the siphonostomes associated with invertebrates are so poorly understood (see Gotto, 1979; Huys and Boxshall, 1991) it is difficult to nominate particular invertebrate associating taxa as having particularly close affiliation with taxa parasitic on vertebrates. Conjecture forwarded by Kabata (1979) and Huys and
Boxshall (1991), however, accurately depicts Asterocheridae, Dirivultidae, and Megapontiidae as primitive taxa associated with invertebrates that possibly are closely related to taxa infecting fishes. Nicothoidae, an associate on other Crustacea, is also notable in that it possesses a little-studied attachment organ much like the frontal filament seen in pennellids, caligiforms, and lernaeopodiforms. Nicothoids are also interesting because they are highly modified copepods bearing a loose overall resemblance to untransformed lernaeopodids and naobranchiids (and presumably other lernaeopodiforms), although the appendages of these groups reveals this similarity to appear superficial (e.g. cf. nicothoid and lernaeopodid morphologies presented in Kabata (1979), Boxshall and Lincoln (1983), and Boxshall and Harrison (1988)). In light of the above, it is apparent that detailed studies of the interfamilial relationships of the siphonostomes associated with invertebrates are needed to better resolve affinities among siphonostome families parasitic on vertebrates, and that molecular studies of siphonostomes may assist in unraveling relationships possibly obscured by many morphological episodes of parallel evolution. Furthermore, the monophyletic status of the siphonostome parasites of vertebrates cannot be fully accepted until a phylogenetic analysis of all siphonostome families is completed. Here it is interesting to note a recent phylogenetic analysis of Poecilostomatoida (Ho, 1991) that indicated that the ten vertebrate infecting poecilostome families originated independently from three different clades of invertebrate infecting families.

SUMMARY AND CONCLUSIONS

In this thesis, a phylogeny for the 18 siphonostome families parasitic on vertebrates has been presented which considers these taxa monophyletic. Although a spectacular set of fossils has firmly established these copepods' presence during the Cretaceous (110 mya), host and habitat distributions are consistent with a possible origin along with the earliest fishes during
the Ordovician (over 441 mya), and that these copepods evolved from ancestors associated with invertebrates.

Siphonostomes that infect vertebrates typically are found attached at specific locations on their hosts. Most copepod distributions remain inexplicably confined, although morphology can sometimes be used to explain realized niches. Contemporary distributions suggest that the branchial chambers and olfactory capsules were the first regions of the vertebrate body colonized. Parasite distribution and host morphology data also suggest that the olfactory capsules of vertebrates may have been derived from some premandibular branchial component and their evolution in turn caused an evolutionary split in some portions of the parasite fauna infecting the branchial chambers of noseless and jawless fishes. The general body surfaces of vertebrates were probably colonized by taxa formerly infecting the gills and olfactory capsules. This invasion may have been facilitated by the development of a new structure of larval attachment, the frontal filament, which securely tethered larvae to their active hosts. In addition to the frontal filament, adults of these larvae appear to have developed two modes of extending this progress in attachment security throughout adulthood. One mode is seen as the derived cephalothorax of many caligiforms, and endows these copepods with the ability to swim powerfully in addition to providing a strong method of suckorial attachment that can be used on the relatively slick external body surfaces of many swift swimming fishes. The second mode is seen in the form of permanently attached adult female copepods, and is realized in two general ways. The first consists of permanent attachment either by encircling a host gill filament with the second maxillae (Naobranchiidae), or by actually anchoring the second maxillae to the host (Lernaeopodidae and Tanypleuridae). The second form involves an ecological shift from ectoparasitism to mesoparasitism (Pennellidae and Sphyriidae).
The primitive life cycle of the siphonostomes infecting vertebrates consists of ten stages. A reduction in the number of molts required to reach adulthood is exhibited by a number of lineages and seems to have been realized through amalgamation of free-living nauplius, and/or parasitic copepodid, chalimus or preadult stages. The first copepodid is maintained throughout all lineages as the initial colonizing stage. Sexual dimorphism ranges from subtle to pronounced, with male modifications seemingly associated with the location and grasping of females, whereas female modifications appear to be directed towards requirements imposed by parasitism and reproduction.

Although most siphonostomes have one host life cycles, at least some pennellids have evolved two host lifestyles. The evolution of these two host cycles seems to have been facilitated by both use of a highly mobile untransformed adult female to infect the definitive host, as well as, by the close ecological proximity of the intermediate and definitive host species either through the use of the same densely schooling species for both portions of the life cycle, or through a predator-prey linked association of two dissimilar species.

Among siphonostome taxa infecting vertebrates, mesoparasitism has apparently evolved several times from ectoparasitic taxa. Phylogenetic data illustrate that once a lineage has been initiated into mesoparasitism, reversal to ectoparasitism is unlikely. Possible requirements of shedding larvae into an open environment may represent the only constraint precluding these mesoparasitic lineages from an endoparasitic lifestyle.

Two siphonostome lineages have successfully invaded fresh water. This significant ecological shift appears to have been facilitated, although not absolutely determined, by a number of morphological, developmental, and ecological traits.
Preliminary studies suggest that siphonostomes have sometimes coevolved with their vertebrate hosts while at other times they have colonized phylogenetically distant yet ecologically similar hosts. Although rich in species, overall numbers suggest that the speciation rate of these copepods seems to have lagged behind that of potential host taxa. No doubt the ever changing array of host species available for infection has and continues to challenge this most successful crustacean taxon of vertebrate parasites.

Evolutionarily, parasitism represents one logical culmination of the intimate association between two species, and considering absolute numbers of species, parasitism may be the most successful heterotrophic lifestyle. As such, parasitism is an ecological rather than a phylogenetic phenomenon. Parasitology, however, makes most sense when lineages are phylogenetically inspected so that the concept of evolution can unify observations gathered from many different biological disciplines. This type of unification has recently accelerated concerning studies of the siphonostomes infecting vertebrates, and its continued practice will advance our understanding of these interesting crustaceans.
REFERENCES


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Ho, J-S. (1989). Phylogeny and biogeography of hakes (Merluccius; Teleostei); A cladistic analysis. Fishery Bulletin, United States 88, 95-104


TABLES
<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Each mandible bearing a prominent row of teeth along one side</td>
</tr>
<tr>
<td>2</td>
<td>Second antennae lacking prominent exopods</td>
</tr>
<tr>
<td>3</td>
<td>Long uniseriate egg sacs</td>
</tr>
<tr>
<td>4</td>
<td>Mandibular palp absent</td>
</tr>
<tr>
<td>5</td>
<td>Fifth thoracic legs incorporated into genital double somite to form genital complex</td>
</tr>
<tr>
<td>6</td>
<td>Chelate second antennae</td>
</tr>
<tr>
<td>7</td>
<td>Fourth thoracic legs highly modified or completely lost</td>
</tr>
<tr>
<td>8</td>
<td>Second maxillae with bifid claws</td>
</tr>
<tr>
<td>9</td>
<td>Maxillipeds absent</td>
</tr>
<tr>
<td>10</td>
<td>Highly modified bilobate fourth legs</td>
</tr>
<tr>
<td>11</td>
<td>Groove on second maxilla delimiting distal portion of brachium from calamus</td>
</tr>
<tr>
<td>12</td>
<td>Frontal organ present, frontal filament used to tether some larval stages to host</td>
</tr>
<tr>
<td>13</td>
<td>Marked reduction in segmentation of first antennae</td>
</tr>
<tr>
<td>14</td>
<td>Labrum and labium fused to form a distinctive mouth tube</td>
</tr>
<tr>
<td>15</td>
<td>Egg arrangement multiseriate</td>
</tr>
<tr>
<td>16</td>
<td>All thoracic legs absent or vestigial</td>
</tr>
<tr>
<td>17</td>
<td>Highly modified grub-like males and untransformed females</td>
</tr>
<tr>
<td>18</td>
<td>Second maxillae used as primary organs of attachment</td>
</tr>
<tr>
<td>19</td>
<td>Second maxillae attached to pull to anchor adult female</td>
</tr>
<tr>
<td>20</td>
<td>Second maxillae long, ribbon-like, used to encircle host tissues, tips attached to trunk</td>
</tr>
<tr>
<td>21</td>
<td>Cephalothorax in form of dorsal shield</td>
</tr>
<tr>
<td>22</td>
<td>Frontal plates on cephalothorax</td>
</tr>
<tr>
<td>23</td>
<td>First maxilla with large dentiform endopod and small exopod with three spiniform setae</td>
</tr>
<tr>
<td>24</td>
<td>First maxilla with reduced digitiform endopod</td>
</tr>
<tr>
<td>25</td>
<td>Corpus maxillipedis squat with modified myxa, subchela at about a right angle to long axis of corpus when closed</td>
</tr>
<tr>
<td>26</td>
<td>Second pedigerous segment incorporated into the cephalothorax</td>
</tr>
<tr>
<td>27</td>
<td>First maxillae distinctly composed of two parts</td>
</tr>
<tr>
<td>28</td>
<td>Third pedigerous segment incorporated into the cephalothorax</td>
</tr>
<tr>
<td>29</td>
<td>Third thoracic legs and interpodal plate modified and fused to form a seal for the cephalothorax</td>
</tr>
<tr>
<td>30</td>
<td>Fourth thoracic legs uniramous</td>
</tr>
</tbody>
</table>

*a Characters refer to condition seen in the adult female unless otherwise noted. Character numbers correspond to those in Figs 21 and 27. Autapomorphic characters are only identified to resolve polyphlogenies or to note characteristics of significance to discussion. For discussion of characters consult text.*
Table 2. Numbers of copepod species infecting various body regions of some sharks in the western North Atlantic (Benz, unpublished data)

<table>
<thead>
<tr>
<th>Shark species a</th>
<th>N</th>
<th>General body surface</th>
<th>Gills and branchial chambers</th>
<th>Olfactory sacs</th>
<th>Buccal chamber</th>
<th>Total body</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bigeye thresher</td>
<td>8</td>
<td>3</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td>Thresher shark</td>
<td>7</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>White shark</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>-</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Shortfin mako</td>
<td>121</td>
<td>2</td>
<td>4</td>
<td>-</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Night shark</td>
<td>15</td>
<td>3</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td>Bignose shark</td>
<td>11</td>
<td>5</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>7</td>
</tr>
<tr>
<td>Tiger shark</td>
<td>9</td>
<td>4</td>
<td>-</td>
<td>4</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Blue shark</td>
<td>78</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>-</td>
<td>9</td>
</tr>
<tr>
<td>Scalloped hammerhead</td>
<td>35</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td>All Sharks b</td>
<td>291</td>
<td>42</td>
<td>42</td>
<td>21</td>
<td>9</td>
<td>100 (33 spp.)</td>
</tr>
</tbody>
</table>

a Common names of sharks according to Robins et al. (1991).
b Copepod species from each region reported as percent of total body value.
FIGURES
FIG. 1 Examples of sexual dimorphism in the adult general habitus of some siphonostomes infecting vertebrates. A, Eudactylinidae; B, Kroyeriidae; C, Dichelesthiidae; D, Pennellidae; E, Trebiidae; F, Phyllothyreus (Edwards, 1840); G, Cecropidae; H, Sphyriidae; I, Lernaeopodidae. Identification labels separate sexes (female always on left); D and I each depict (left to right) untransformed adult female, transformed adult female, and adult male. For explanation see text. Figures modified from Kabata and Cousens (1973) and Kabata (1979). Scale bars represent: 0.5 mm on A, B, D (untransformed female and male), and I; 2.0 mm on C, D (transformed female), E, F, G, and H.
FIG. 2 Ecological summary cladogram of Eudactylinidae genera, considering from top to bottom: host group, lifestyle, and general attachment location. Phylogenetic relationships of copepods as proposed by Deets and Ho (1988), ecological data from numerous primary sources. Bladders on cladogram denote synapomorphic support from cladogram of Deets and Ho (1988).
FIG. 3 Two *Nemesis* species infecting different regions of the gill filaments of lamnid sharks. Top, *Nemesis lamna* Risso, 1826 infecting gill filaments of the shortfin mako (*Isurus oxyrinchus* Rafinesque, 1810). *Nemesis lamna* usually attaches at the dorsal (this instance) and ventral aspects of a gill arch some distance in from the tip of a gill filament; Bottom, *Nemesis robusta* (van Beneden, 1851) infecting gill filaments of the thresher shark (*Alopias vulpinus* (Bonnaterre, 1758)). Note how *Nemesis robusta* aggregate about the gill arch and attach about the efferent tips of the gill filaments. Top from Benz (1980), Bottom from Benz and Adamson, 1990).
FIG. 4  *Kroyeria carchariaeglauci* Hesse, 1879 females parasitic on gills of a blue shark (*Prionace glauca* (L., 1758)). Top, individual residing in water channel between two gill filaments. Note chelate second antennae grasping the host substrate and the dorsal stylet projecting upwards toward the secondary lamellae; Bottom, a dorsal stylet propped against a secondary lamella of a gill filament. Top and Bottom from sectioned material.
FIG. 5 *Kroyeria caseyi* Benz and Deets, 1986 females embedded in the interbranchial septum of a night shark (*Carcharhinus signatus* (Poey, 1868). Note the collar of host tissue surrounding the parasites where they penetrate the host (from Benz and Deets, 1986).
FIG. 6  Sectioned elasmobranch gill (diagrammatic) illustrating niches typically inhabited by some siphonostomes (clockwise from top left): Pandarus cranchii Leach, 1819 on gill arch; Eudactylinodes uncinata (Wilson, 1909) and Bariaka alopiæ Cressey, 1966 on secondary lamellae; Nemesis lamna Scott, 1929 and Lernaeopodina longimana (Olsson, 1869) on capping tissue surrounding efferent arteriole; Phyllothyreus cornutus (Edwards, 1840) superficially on interbranchial septum; Paeon vaissieri Delamare Deboutteville and Nunes-Ruivo, 1954 and Kroeyeria caseyi Benz and Deets, 1986 partially embedded in interbranchial septum; Gangliopus pyriformis Gerstaecker, 1854 on secondary lamellae; Kroeyeria lineata van Beneden, 1853 in water channel and on secondary lamellae; Lernaeopodina longimana and Anthosoma crassum (Abildgaard, 1794) on gill arch. Distribution records of parasites from the author's personal observations. Abbreviations: GA, gill arch; GF, gill filament; IS, interbranchial septum.
FIG. 7 *Lemanthropus pomatomi* Rathbun, 1887 female from gill filaments of a bluefish (*Pomatomus saltatrix* L., 1758). Note how edges of cephalothorax curl ventrally to form a tunnel-like pathway through which one host gill filament can pass. The claw-like second antennae and chelate maxillipeds can be seen positioned along this pathway, where they secure the filament in their grasps. Note also the highly modified third pair of thoracic legs which form a more posterior passageway which assists in attachment and in maintaining the parasite in line with the gill filament in the face of respiratory water flow.
FIG. 8 Sectioned teleost gill (diagrammatic) illustrating niches typically inhabited by some siphonostomes (clockwise from top left): Clavella adunca (Strøm, 1762) and Caligus productus Dana, 1852 on gill arch and gill rakers; Lernanthropus species on capping tissue of surrounding efferent arteriole; Naobranchia species encircling gill filament; Lernanthropus species on tissue surrounding afferent arteriole; Clavella adunca on capping tissue surrounding efferent arteriole; Hatschekia species on secondary lamellae; Haemobaphes species and Lernaeocera species cephalothorax and portion of trunk penetrating afferent artery and often coursing to heart. Distribution records of parasites from the author's personal observations. Abbreviations: GA, gill arch; GF, gill filament.
FIG. 9 *Pennella instructa* Wilson, 1917; mesoparasitic females embedded in swordfish (*Xiphias gladius* L., 1758). Top, posterior body portions of two females trailing free from host (arrow marks point of parasite entry); Bottom, close-up of two different females showing abdominal plumes which give the external portion of these parasites an arrow's shaft appearance. Length of white ruler approximately 15 cm.
FIG. 10 Ecological summary cladogram of Pennellidae genera, considering from top to bottom: definitive host group, intermediate host group, and lifestyle. Phylogenetic relationships of copepods as proposed by Boxshall (1986). Ecological data from numerous primary sources. Bladders on cladogram denote synapomorphic support from cladogram of Boxshall (1986).
FIG. 11 Ventral view of female *Pandarus bicolor* Leach, 1816 showing major structures of attachment. Abbreviations: a2, second antenna; ap1, adhesion pad associated with first antenna; ap2, adhesion pad associated with second antenna; ap3, postoral adhesion pad; ap4, adhesion pad associated with first free thoracic segment; mxp, maxilliped. Electron micrograph.
FIG. 12  Second maxillae of some pandarid species. Top left, Pandarus bicolor Leach, 1816, adult female; Top right, clavus of P. bicolor, adult female; Bottom left, Echthrogaleus coleoptratus (Guerin-Meneville, 1837), adult female; Bottom right, Echthrogaleus sp. copepodid. See text for explanation. Abbreviations: cl, clavus; cr, crista; ?, projection crowned with this spinules.
FIG. 13 Cephalothorax rim of two pandarid copepods. Top, inner edge of female *Echthrogaleus coleoptratus* (Guerin-Meneville, 1837) cephalothorax. Note marginal membrane and basal rank of spines; Bottom, inner edge of female *Pandarus bicolor* Leach, 1816 cephalothorax. Note how border consists only of membranous rays that become amalgamated into spines along the outer edge. *Echthrogaleus coleoptratus* typically resides on portions of a shark's body where the placoid scales are very fine (see Benz, 1986) and where the combination of a marginal membrane and row of spines about its cephalothorax would seem highly useful in both sealing the cephalothorax to the host and in gripping the host. *Pandarus* species are normally found attached to their shark hosts where the placoid scales are large (see Benz, 1981, 1992) and where a row of stout spines about the cephalothorax would serve to assist in gripping the host.
FIG. 14 Female *Phyllothyreus cornutus* (Edwards, 1840) attached to blue shark (*Prionace glauca* (L., 1758)) interbranchial septum. Note claw-like second antennae deeply penetrating host. From sectioned material.
FIG. 15 Female Pandarus bicolor Leach, 1816 maxillipeds. Top, empty maxilliped; Bottom, maxilliped clasping a host placoid scale. Note how bifid tip of claw meets neck of placoid scale and how the grasping action of the maxilliped forces the scale's crown against the myxal pad and lateral myxal projection. Top and Bottom electron micrographs.

Abbreviations: cl, claw; Imp, lateral myxal projection; mp, myxal pad; ps, placoid scale.
FIG. 16  Second antenna of female *Perissopus oblongatus* (Wilson, 1908). The toothed apex is buried deep into host tissues to secure this species. Electron micrograph.
FIG. 17 Female *Perissopus dentatus* Steenstrup and Lütken, 1861. Top, lateral view of cephalothorax showing maxilliped still attached to many host placoid scales; Bottom, maxilliped free of placoid scales showing scale impressions in the gluey substance which covers the myxal pad. Top and Bottom electron micrographs.
FIG. 18 Cluster of ovigerous female *Alebion crassus* Wilson, 1932 below trailing edge of the first dorsal fin of a scalloped hammerhead (*Sphyrna lewini*) (Griffith and Smith, 1834).
FIG. 19  *Alebion lobatus* Cressey, 1970 copepodids infecting a sandbar shark (*Carcharhinus plumbeus* (Nardo, 1827)). Top, scatter of perforations caused by invading copepodids; Bottom, electron micrograph of copepodid nestled in a lesion surrounded by placoid scales. Top and Bottom from Benz (1989).
FIG. 20 Large gathering of *Caligus productus* Dana, 1852 on the roof of the buccal cavity of a yellowfin tuna (*Thunnus albacares* (Bonnaterre, 1788)).
FIG. 21 Hypotheses of phylogenetic relationships of siphonostome families parasitic on vertebrates. Numbers refer to character states listed in Table 1, asterisks denote homoplastic characters, character reversals are indicated by solid circles (copepods redrawn from Kabata, 1966a, 1968, 1969b, 1979; Ho, 1987).
FIG. 22 Mouth tubes of two elasmobranch infecting pandarid siphonostomes. A, *Pandarus satyrus* Dana, 1852, female; B, *Dinemoura latifolia* (Steenstrup and Lütken, 1861), female. Note how the mouth tube of *Dinemoura* possesses a fringing skirt seemingly capable of sealing the tip to the host, while in *Pandarus* the tip is pointed and possesses robust spines which appear able to anchor the mouth tube within host tissues. Note also that the invasive tip of *Pandarus* is considerably narrower than the sealing tip of *Dinemoura*. A and B drawn from electron micrographs. Abbreviations: lb, labium; lr, labrum; m, mandible.
FIG. 24 Sternal elements of two caligiform copepods. Top, sternal furca of female *Paralebion elongatus* Wilson, 1911; Bottom, sternal projection of female *Demoleus heptapus* (Otto, 1821). Note the corrugated tip of this projection and be aware that *D. heptapus* infects the placoid scale studded surface of sharks where the application of such a rough tip probably assists the copepod to maintain a stationary position in the face of passing water. Top and Bottom electron micrographs.
FIG. 25 Maxilliped of female *Phyllophyreus cornutus* (Edwards, 1840) grasping epithelial tissue of the interbranchial septum of a blue shark (*Prionace glauca* (L., 1758)). Note that the myxal region of this pandarid appears distally displaced and that it is grasping a host surface devoid of placoid scales. From sectioned material.
FIG. 26 Life cycle summaries for siphonostomes parasitic on vertebrates. Vertical lines denote molts, arrows denote considerable development without molting (i.e. metamorphosis). See text for further explanation and primary references. Figure entries as follows: C, copepodid; CH, chalimus; ECH, ephemeral chalimus (preadult) using frontal filament for molting and exhibiting an untethered condition for most of its existence; IE, nauplius development passed while in egg; inf, first or only colonizing stage; P, pupaform larva; TF, transformed adult female; UT, untransformed adult male and female; UTM, untransformed adult male; X, stage present; ?C, copepodid stage possibly observed; -, stage considered absent.
<table>
<thead>
<tr>
<th></th>
<th>Nauplius</th>
<th>Copepodid</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>inf</td>
</tr>
<tr>
<td>Eudactyliniidae</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kroyeriidae</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatschekiidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudocycniidae</td>
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<td>Hyponeoidae</td>
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<tr>
<td>Lernanthropidae</td>
<td>X</td>
<td>X</td>
<td>C</td>
</tr>
<tr>
<td>Dicholesthiidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pennellidae I</td>
<td>X</td>
<td>X</td>
<td>C</td>
</tr>
<tr>
<td>Pennellidae II</td>
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<td></td>
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</tr>
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<td>Sphyriidae</td>
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<td>C</td>
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<td>IE</td>
<td>C</td>
<td>CH</td>
</tr>
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<td>X</td>
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<td>C</td>
</tr>
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<td>Naobranchiidae</td>
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<tr>
<td>Caligidae</td>
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</tr>
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</table>
FIG. 27  Ecological summary cladogram for siphonostome families parasitic on vertebrates (considering from top to bottom: environmental habitat, major host groups, lifestyle, and general attachment location on host). Entries in parentheses denote relatively minor representation. Ecological data from numerous primary records. Phylogenetic relationships of copepods as proposed in Fig. 21. Numbers on phylogeny correspond to supporting morphological characters (see Table 1), homoplasious characters are denoted by asterisks, character reversals are indicated by solid circles.
FIG. 28 Comparison of the gills and olfactory sacs of elasmobranchs. Top, series illustrating (left to right) how a gill can be modified to form an olfactory sac. Arrows denote directions of water flow; Bottom, gill (left) and olfactory sac (right). Note how both gills and olfactory sacs possess orderly arrangements of serially repeating components (i.e. filaments and lamellae) radiating from a supporting rod (i.e. gill arch and rachis). Note also how kroyeriid and some pandarid copepods infect similar (homologous?) regions within each environment. Abbreviations: GA, gill arch; GF, gill filament; GSL, gill secondary lamella; K, kroyeriid copepod; OF, olfactory filament; OSL, olfactory secondary lamella; P, pandarid copepod; R, rachis; WC, water channel. Figure prepared with data from Benz (1984, in preparation).
APPENDIX
Appendix 1. List of species and collections examined during the phylogenetic analysis of siphonostomes parasitic on vertebrates. Abbreviations: ARCHML, Atlantic Reference Centre Huntsman Marine Laboratory (St. Andrews, N.B.); BCPM, British Columbia Provincial Museum; BENZ, Personal collection of the author; BMNH, British Museum of Natural History; DEETS, Personal collection of Gregory B. Deets (University of British Columbia); IZAWA, Personal collection of Kunihiko Izawa (Mie University); SAMA, South Australian Museum in Adelaide; SAMCT, South African Museum (Cape Town); SHUNO, Collection of Sueo Shiino (Mie University); USNM, United States National Museum.

Eudactylinidae:


**Eudactylinodes keratophagus** Deets and Benz, 1986: USNM Coll. Nos. 231378 (Holotype), 231379 (Paratypes).


Kroyeriidae:


**Kroyeria caseyi** Benz and Deets, 1986: USNM Coll. No. 231376 (Holotype); BENZ Coll. Nos. B10 (Allotype), B11 (Paratypes).


**Kroyerina elongata** Wilson, 1932: BENZ Coll. Nos. B17, B70, B71, B72, B73, B424.


Pseudocycnidae:

Dichelesthiidae:


**Kabatarina pattersoni** Cressey and Boxshall, 1989: BMNH Coll. Nos. 63466, 63467, 63468, 63469, 63470, 63625, 63626, 63627.

Lernanthropidae:


Pennellidae:


**Lernaeenicus longiventris** Wilson, 1917: BENZ Coll. No. B301.

**Lernaeenicus radiatus** Le Sueur, 1824: BENZ Coll. No. A148.

**Lernaeenicus** sp.: BENZ Coll. No. B414.


**Prixocephalus** sp.: BENZ Coll. No. A164.

Dissonidae:

**Dissonus spinifer** Wilson, 1906: USNM Coll. No. 56592.

Pandaridae:

**Demoleus heptapus** (Otto, 1821): BMNH Coll. Nos. 1911.11.8.48111, 1911.11.8.48112; USNM Coll. No. 60465.


Echthrogaleus disciarai Benz and Deets, 1987: USNM Coll. Nos. 231380 (Holotype), 231381 (Allotype), 231382 (Paratype), 231383 (Paratype).


Cecropidae:

*Entepherus* *laminipes* Bere, 1936: DEETS unaccedioned specimens.


Trebiidae:

Euryphoridae:


*Alebion* *gaber* Wilson, 1905: SAMA Coll. Nos. TC2290, TC2293.


*Gloiopotes* *watsoni* Kirtisinghe, 1934: BENZ Coll. Nos. A63, A64.

*Paralebion* *elongatus* Wilson, 1911: BENZ Coll. Nos. B261, B262, B263; USNM Coll. No. 256546.

Caligidae:
*Caligus* *chelifera* Wilson, 1905: BENZ Coll. No. A53.


*Caligus* *curtus* Müller, 1785: BENZ Coll. Nos. A89, A217.


Sphyriidae:

**Opimia** sp.: BENZ Coll. No. A403.

**Periplexis lobodes** Wilson, 1919: BENZ Coll. No. A132.

Lernaeopodidae:


**Albionella kabatai** Benz and Izawa, 1990: USNM Coll. No. 254426 (Holotype).

**Albionella oviformis** (Shiino, 1956): SHIINO Coll. No. 480 (Holotype).


**Nectobrachia indivisa** Fraser, 1920: BENZ Coll. Nos. B336, B337.

**Salmincola californiensis** (Dana, 1852): BENZ Coll. No. B310.

Naobranchiidae

**Naobranchia lizae** (Krøyer, 1864): BENZ Coll. No. B149.