

DEVELOPMENTAL PATTERNS IN NUMBERS OF RAMAL
SEGMENTS OF COPEPOD POST-MAXILLIPEDAL LEGS

BY

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RÉSUMÉ

Les changements dans le nombre des articles des rames des pattes post-maxillipédiennes au cours du développement ont été relevés chez 185 genres de copépodes, d'après la littérature. Un modèle commun de développement pour les pattes 1-4 a été identifié chez 31 genres appartenant à 17 familles rangées dans 5 des 9 ordres.

Des modèles différents de développement conduisant à des nombres similaires d'articles, convergences de développement, sont relevés, alors que des réductions du nombre de ces articles sont constatées parmi des genres répartis en 5 ordres. L'apparition et le développement des pattes post-maxillipédiennes des copépodes suggèrent des similarités avec les structures homéotiques des autres Arthropodes. La prise en compte des convergences de développement et de réduction dans un modèle homéotique peut compliquer l'usage des séquences des nombres d'articles des rames en tant que séries de transformation dans les analyses phylogénétiques.

INTRODUCTION

A common problem in the reconstruction of copepod phylogeny involves understanding the evolutionary transformation of varying numbers of apparently repeating segments or elements that are present among a group of presumed related species. For copepodologists the usual analytical operation is to determine the largest number of elements represented among a group of species, and assume that this number is the primitive condition within that group. Fewer numbers in the sequence are then supposed to have resulted from a subsequent genetic process that leads to successive element fusion or loss, and an evolutionary transformation (a reduction sequence) of derived character states in which, for example, three segments or setae are always derived from four, which in turn are always derived from five, etc.

The above approach may suffer from problems in its assumptions and consequences: (1) Evolutionary convergence in decreasing element numbers may confound the presumed simple linearity of reduction sequences. Furthermore, Hocht & Edwards (1976) have suggested that reduction sequences should be regarded as the weakest of five categories of character transformations. These authors inferred that reductions are an easily-effected process. If reduction sequences are easily-effected and widespread among a group of lineages, con-

tinued encounters with converging sequences should be expected, and their value in phylogenetic analyses may be compromised (see discussions of Boxshall & Tiemann in Tiemann, 1984). (2) The above approach may confuse phenotypic loss by gene loss with phenotypic loss by gene repression; this latter case may vitiate the presumed direction of reduction sequences. When genes governing a character state are lost from an organism's genome, modifications of that character state should not appear again among its descendants. However, character states lost through repression of gene action may conceivably recur among descendants if the repressing system is altered. (3) Finally there are some unusual teleological implications for the evolution of reduction sequences; one logical end point for continued loss of elements is a single-celled organism (see comments of Soto in Kabata, 1986).

Segmentation patterns for rami of post-maxillipedal appendages seem to provide an excellent study of reduction sequences in copepods. About 8400 species of copepods belong to 180+ families in nine orders (Bowman & Abele, 1982; Boxshall & Lincoln, 1983; Ho, 1984; Fosshagen & Iliffe, 1985; Humes, 1986a). The number of exopodal and endopodal segments comprising post-maxillipedal appendages in adults (the preferred stage for phylogenetic analyses) varies throughout the nine orders. During development numbers of post-maxillipedal legs, and of their exopodal and endopodal segments, also vary through a series of naupliar and copepodid stages.

In this paper developmental patterns in numbers of ramal segments are surveyed from the literature and compared among various copepod genera. Information about these patterns is used to assess developmental convergences in segment numbers of adult copepods, as these convergences may reflect the ease in which similar evolutionary transformations may be effected. Discovery of examples of reductions in segment numbers during development provides direct phenotypic evidence of the effects of gene repression. Some consequences of developmental convergence and gene repression in establishing transformation series will be outlined by noting briefly the similarities of post-maxillipedal leg development to well-studied homeotic structures of *Drosophila*. Information about genetic control of the development of homeotic structures will facilitate a discussion of gene repression vs. gene loss models, and of the implication of these models to the teleology of reduction sequences.

METHODS

Information about the development of post-maxillipedal appendages was obtained for 185 genera (three of uncertain familial affinity) in 74 copepod families (one of uncertain ordinal affinity) listed in table I. For a genus to be included in this study at least two contiguous stages of leg development had to be known. Orders, families within orders, and genera within families are listed alphabetically in table I. In the following text, genera are listed in the

order they appear in table I. Segment counts were taken from descriptions or illustrations; no attempt was made to qualify segment numbers for known or presumed appendage function, nor were segment homologies established by size or number, or position of armature.

If similar development of post-maxillipedal legs has been described several times for the same species in a represented genus, the paper with the most complete descriptions of post-maxillipedal legs or one which represents the most recent, and thus usually more accessible account, is cited. Two or more papers may be listed for the same genus if together they provide more complete information about development or resolve differences among several accounts of development of the same species; if development of two or more congeneric species differs, papers recording each are listed. The various cited studies often differed in the amount of descriptive detail. Furthermore, comparisons among papers are complicated because not all authors had every developmental stage available for study. Many observations of early sexual dimorphism or copepodid polymorphism often were omitted, and authors interpreted various structures (appendage bud, appendage segment or segment boundary) differently.

TABLE I

Sources of information for post-maxillipedal leg development of copepod genera (* = nauplii and/or early copepodids undescribed, # = later copepodids undescribed, @ = adult only). Totals: 74 families, 185 genera

CALANOIDA 19 families, 45 genera		
Acartiidae	<i>Acartia</i>	by Grandori (1912) and Trujillo-Ortiz (1986)
Aetideidae	<i>Paracartia</i>	by Vilela (1972, as <i>Acartia</i>)
	<i>Aetideopsis</i>	by Mazza (1965*, as <i>Pseudaetideus</i>) and Sars (1925)@
	<i>Bradyidius</i>	by Shih et al. (1981)*
	<i>Chiridius</i>	by Matthews (1964) and MacLellan & Shih (1974)*
Calanidae	<i>Euchirella</i>	by Sewell (1929)* and Mazza (1965)*
	<i>Gaetanus</i>	by Mazza (1965)*
	<i>Calanoides</i>	by Vervoort (1946)* # and Tanaka (1938)@
	<i>Calanus</i>	by Campbell (1934)
	<i>Neocalanus</i>	by Vervoort (1946)* and Sars (1925)@
Centropagidae	<i>Undinula</i>	by Björnberg (1966) # and Sewell (1929)*
	<i>Boeckella</i>	by Fairbridge (1945a)
	<i>Calamoecia</i>	by Fairbridge (1945b, as <i>Brunella</i>)
Clausocalanidae	<i>Centropages</i>	by Lawson & Grice (1970)
	<i>Gladioferens</i>	by McKinnon & Arnott (1985)
	<i>Clausocalanus</i>	by Heron & Bowman (1971)*
	<i>Ctenocalanus</i>	by Heron & Bowman (1971)*

Diaptomidae	<i>Aglaodiaptomus</i>	by Kamal & Armitage (1967, as <i>Diaptomus</i>)
	<i>Diaptomus</i>	by Gurney (1931)
	<i>Leptodiaptomus</i>	by Comita & Tommerdahl (1960, as <i>Diaptomus</i>)
	<i>Megadiaptomus</i>	by Ranga Reddy & Rama Devi (1985)
	<i>Skistodiaptomus</i>	by Comita & McNett (1976, as <i>Diaptomus</i>)
Eucalanidae	<i>Eucalanus</i>	by Johnson (1937) # and Esterly (1905) @
	<i>Rhincalanus</i>	by Schmaus (1971) # and Schmaus & Lehnhofer (1927) * # and Giesbrecht (1892) @
Euchaetidae	<i>Euchaeta</i>	by Campbell (1934)
Heterorhabdidae	<i>Heterorhabdus</i>	by Mazza (1965) * and Sars (1925) @
Megacalanidae	<i>Bathycalanus</i>	by Vervoort (1946) * and With (1915) @
	<i>Megacalanus</i>	by Vervoort (1946) * and Sars (1925) @
Metridinidae	<i>Gaussia</i>	by Sewell (1932) *
	<i>Metridia</i>	by Pinero di Verdinelli (1981) *
	<i>Pleuromamma</i>	by Ferrari (1985) *
Paracalanidae	<i>Paracalanus</i>	by Lawson & Grice (1973)
Phaennidae	<i>Xanthocalanus</i>	by Matthews (1964)
Pontellidae	<i>Calanopia</i>	by Li & Fang (1984) # and Sewell (1932) @
	<i>Labidocera</i>	by Gibson & Grice (1977)
	<i>Paralabidocera</i>	by Johnson (1934b) #, as <i>Epilabidocera</i> and Esterly (1924) @
	<i>Pontella</i>	by Gibson & Grice (1976)
Pseudodiaptomidae	<i>Pseudodiaptomus</i>	by Grice (1969) and Katona (1971) and Cicchino (1975)
Scolecithricidae	<i>Scottocalanus</i>	by Sewell (1929) * and Scott (1909) @
Spinocalanidae	<i>Monacilla</i>	by Vervoort (1946) * and Sars (1925) @
Temoridae	<i>Epischura</i>	by Humes (1955) # and Marsh (1933) @
	<i>Eurytemora</i>	by Grice (1971)
	<i>Heterocope</i>	by Elster (1932)
	<i>Temora</i>	by Parameswaran Pillai (1975) and Li & Fang (1983) # and Koga (1984) #
Tortanidae	<i>Tortanus</i>	by Johnson (1934)
CYCLOPOIDA 6 families, 30 genera		
Ascidicolidae	<i>Ascidicola</i>	by Illg & Dudley (1980) # and Sars (1921b) @
	<i>Enterocola</i>	by Canu (1892) #
	<i>Enteropsis</i>	by Illg & Dudley (1980) #
	<i>Haplosaccus</i>	by Ooishi (1980) # and Ooishi & Illg (1977)
	<i>Haplostoma</i>	by Ooishi (1980) # and Ooishi & Illg (1977) @
	<i>Haplostomella</i>	by Ooishi (1980) # and Ooishi & Illg (1977) @
	<i>Zanclopus</i>	and Anderson & Rossiter (1968) # by Calman (1908)

Cyclopidae	<i>Acanthocyclops</i>	by Lucks (1927, as <i>Cyclops</i>)	
	<i>Apocyclops</i>	by Valderhaug & Kewalramani (1979) # and Dussart (1982)@	
	<i>Cyclops</i>	by Claus (1893)	
	<i>Diacyclops</i>	by Amores-Serrano (1978, as <i>Cyclops</i>)	
	<i>Ectocyclops</i>	by Carvalho (1971)	
	<i>Eucyclops</i>	by Auvray & Dussart (1966) # and Dussart (1982)@	
	<i>Graeteriella</i>	by Lescher-Moutoué (1973) # and Kiefer (1957)@	
	<i>Halicyclops</i>	by Candeias (1966)	
	<i>Macrocylops</i>	by Defaye (1984)	
	<i>Mesocyclops</i>	by Amores-Serrano (1978)	
	<i>Speocyclops</i>	by Lescher-Moutoué (1966) # and Chappuis & Kiefer (1952)@	
	Cyclopinidae	<i>Cyclopina</i>	by Goswami (1977a)
	Lernacidae	<i>Lamproglena</i>	by Kuang (1962) # and Sproston et al. (1950)@
<i>Lernaea</i>		by Grabda (1963) and Nakai (1927)	
Notodelphyidae	<i>Mesolamproglena</i>	by Kuang (1980)*	
	<i>Bonnierilla</i>	by Canu (1892) #	
	<i>Doroixys</i>	by Canu (1892) #	
	<i>Doropygus</i>	by Dudley (1966)	
	<i>Notodelphys</i>	by Dudley (1966)	
	<i>Pachygygus</i>	by Hipeau-Jacquotte (1978)	
	<i>Pygodelphys</i>	by Dudley (1966)	
Oithonidae	<i>Scolecodes</i>	by Dudley (1966)	
	<i>Oithona</i>	by Uchima (1979)	

HARPACTICOIDA 19 families, 43 genera

Ameridae	<i>Nilocra</i>	by Abraham & Gopalan (1975)
Balaenophilidae	<i>Balaenophilus</i>	by Aurivillius (1879)
Canthocamptidae	<i>Antrocamptus</i>	by Rouch (1960) # and Chappuis & Rouch (1960)@
	<i>Bryocamptus</i>	by Carter & Bradford (1972) # and Coker (1934)@
	<i>Canthocamptus</i>	by Itô & Takashiro (1980) # and Itô & Takashiro (1981)@
	<i>Elaphoidella</i>	by Carter & Bradford (1972) # and Coker (1934)@
	<i>Moraria</i>	by Carter & Bradford (1972) # and Carter (1944)@
Canuellidae	<i>Canuella</i>	by Vincx & Heip (1979)
Cletodidae	<i>Sunaristes</i>	by Codreanu & Mack-Fira (1961)
	<i>Cletocamptus</i>	by Bourguet (1986a)* and Bourguet (1986) #
Cylindropsyllidae	<i>Arenopontia</i>	by Chandrasekhara Rao (1967)
Diosaccidae	<i>Leptastacus</i>	by Krishnaswamy (1955) #
	<i>Amphiascoides</i>	by Rosenfield (1967)
	<i>Amphiascus</i>	by Rosenfield (1967)
	<i>Paramphiascella</i>	by Rosenfield & Coull (1974)*
	<i>Robertgurneya</i>	by Rosenfield (1967)
	<i>Robertsonia</i>	by Rosenfield (1967)
Ectinosomatidae	<i>Schizopera</i>	by Rosenfield (1967)
	<i>Microsetella</i>	by Hirakawa (1974)

Harpacticidae	<i>Harpacticella</i>	by Itô (1977)*
	<i>Harpacticus</i>	by Itô (1971)* and Castel (1976)
	<i>Paratigriopus</i>	by Itô (1976) # * and Itô (1969)@
	<i>Tigriopus</i>	by Itô (1970) # and Mori (1938)@
	<i>Zaus</i>	by Itô (1976) # and Itô (1974)*
Laophontidae	<i>Laophonte</i>	by Raibaut (1963) and Goswami (1977b)
	<i>Platychelipus</i>	by Barnett (1966)* and Sars (1911)@
Longipediidae	<i>Longipedia</i>	by Onbé (1984)
Metidae	<i>Metis</i>	by Nichols (1941) # and Vervoort (1964)@
Miraciidae	<i>Macrosetella</i>	by Krishnaswami (1951) # and Wilson (1932)@
	<i>Miracia</i>	by Björnberg (1965) # and Boxshall (1979)@
Parasthenelidae	<i>Parasthenelia</i>	by Brian (1921*, as <i>Microthalestris</i>) and Sars (1905@, as <i>Microthalestris</i>)
Peltidiidae	<i>Alteutha</i>	by Brian (1922)
	<i>Sacodiscus</i>	by Humes (1960)
Porcellidiidae	<i>Porcellidium</i>	by Bocquet (1948)
Tachidiidae	<i>Euterpina</i>	by Haq (1965)
	<i>Tachidius</i>	by Teare (1978) # and Sars (1909)@
Thalestridae	<i>Diarthrodes</i>	by Fahrnbach (1962)
	<i>Eudactylopus</i>	by Itô (1974)*
	<i>Paradactylopodia</i>	by Brian (1921*, as <i>Dactylopusia</i>) and Sars (1905@, as <i>Dactylopusia</i>)
Tisbidae	<i>Thalestris</i>	by Harding (1954)
	<i>Scutellidium</i>	by Brian (1919*, as <i>Psamathe</i>) and Branch (1974)
	<i>Tisbe</i>	by Johnson & Olsen (1940) and Chua (1975)
	<i>Tisbintra</i>	by Ummerkutty (1960)
MISOPHRIOIDA 1 family, 2 genera		
Misophriidae	<i>Benthomisophria</i>	by Boxshall & Roe (1980)*
	<i>Misophria</i>	by Gurney (1933) # and Sars (1903)@
MONSTRILLOIDA 2 families, 3 genera		
Monstrillidae	<i>Cymbasoma</i>	by Malaquin (1901, as <i>Haemocera</i>)
	<i>Monstrilla</i>	by Pelseneer (1914)
Thaumatopsyllidae	<i>Thaumatopsyllus</i>	by Bresciani & Lützen (1962 #, as <i>Thespesiopsyllus</i>) and Sars (1921a)@
POECILOSTOMATOIDA 16 families, 28 genera		
Chondracanthidae	<i>Acanthochondria</i>	by Heegaard (1947) and Izawa (1986b)
	<i>Praecidochondria</i>	by Izawa (1986b) # * and Izawa (1975)@
	<i>Pseudacanthocanthopsis</i>	by Izawa (1986b) # * and Izawa (1975b)@

Clausidiidae	<i>Leptinogaster</i>	by Humes (1986b)*
Corycaidae	<i>Corycaeus</i>	by Gibson & Grice (1978)*
Cucumaricolidae	<i>Cucumaricola</i>	by Peterson (1958)
Ergasilidae	<i>Ergasilus</i>	by Zmerzlaya (1972) and Ben Hassine (1983) and Varella (1985)
	<i>Neoergasilus</i>	by Urawa et al. (1980)# and Urawa et al. (1980b)*
	<i>Sinergasilus</i>	by Mirzoeva (1973)
	<i>Thersitina</i>	by Gurney (1913) and Kabata (1979)
Gastrodelphyidae	<i>Sabellacheres</i>	by Dudley (1964)
Lichomolgidae	<i>Aspidomolgus</i>	by Humes (1969)*
	<i>Lichomolgus</i>	by Costanzo (1968)* and Costanzo (1969)#
	<i>Neanthessius</i>	by Izawa (1986b)#* and Izawa (1976a)@
Mycolidae	<i>Ostricola</i>	by Kô (1969)*
	<i>Midicola</i>	by Do et al. (1984, as <i>Pseudomycolia</i>)
	<i>Panaietis</i>	by Izawa (1986b)#* and Izawa (1976a)@
Mytilicolidae	<i>Mytilicola</i>	by Costanzo (1959) and Pesta (1907)* and Caspers (1939)
	<i>Trochicola</i>	by Bocquet et al. (1963)
Oncacidae	<i>Onciaea</i>	by Malt (1982)
Philichthyidae	<i>Colobomatus</i>	by Izawa (1975a)# and Izawa (1974)@
Philoblennidae	<i>Philoblenna</i>	by Izawa (1986a)#* and Izawa (1976a)@
Sabelliphilidae	<i>Modiolicola</i>	by Costanzo (1984) and Sars (1918)@
	<i>Paranthessius</i>	by Briggs (1977)#* and Humes & Stock (1973)@ and Illg (1949)*
Sarcotacidae	<i>Sarcotaces</i>	by Izawa (1973)# and Komai (1924)@
Splanchnotrophidae	<i>Ismaila</i>	by Belcik (1981)*# and Ho (1987)*# and Ho (1981)@
Taeniacanthidae	<i>Anchistrotos</i>	by Izawa (1986b)
	<i>Taeniacanthus</i>	by Izawa (1986a)*
SIPHONOSTOMATOIDA 10 families, 31 genera		
Caligidae	<i>Caligus</i>	by Kabata (1972)# and Parker & Margolis (1964)@ and Izawa (1969) and Ben Hassine (1983)
	<i>Lepeophtheirus</i>	by Lewis (1963)* and Boxshall (1974b)* and Boxshall (1974a)@
Cancerillidae	<i>Cancerilla</i>	by Carton (1968)
Dissonidae	<i>Dissonus</i>	by Anderson & Rossiter (1969)# and Kabata (1966)@
Dyspontiidae	<i>Dyspontius</i>	by Canu (1892)*# and Sars (1915)@
Lernaeopodidae	<i>Achtheres</i>	by Zandt (1935)*# and Kabata (1979)@

	<i>Aiella</i>	by Kawatow et al. (1980)
	<i>Basanistes</i>	by Kollar (1835)
	<i>Clavella</i>	by Gurney (1934)# and Kabata (1979)@
	<i>Salmincola</i>	by Kabata & Cousens (1973)
	<i>Tracheliastes</i>	by Vejdovský (1877)# and Kabata (1979)@
	<i>Vanbenedenia</i>	by Kabata (1964)*#
Lernanthropidae	<i>Lernanthropus</i>	by Cabral et al. (1984)
Nicothoidae	<i>Aspidoecia</i>	by Hansen (1897)
	<i>Choniorhiza</i>	by Boxshall & Lincoln (1983)
	<i>Choniosphaera</i>	by Connolly (1929)
	<i>Chonistoma</i>	by Giard & Bonnier (1889)
	<i>Diexanthema</i>	by Ritchie (1975)
	<i>Hansenulus</i>	by Heron & Damkacir (1986)
	<i>Homeoscelis</i>	by Hansen (1897)
	<i>Mysidion</i>	by Hansen (1897)
	<i>Nicothoe</i>	by Gurney (1930)# and Leigh-Sharpe (1926)@
	<i>Rhizorhina</i>	by Lincoln & Boxshall (1983)
	<i>Sphaeronella</i>	by Giard & Bonnier (1889)
	<i>Sphaeronellopsis</i>	by Bowman & Kornicker (1967) and Hansen (1897)
Pennellidae	<i>Cardiodectes</i>	by Ho (1966)* and Perkins (1983)* and Wilson (1917)@
	<i>Lernaenicus</i>	by Schram (1979)# and Kabata (1963) and Kabata (1979)@
	<i>Lernaocera</i>	by Sproston (1942)
Saccopsidae	<i>Sarcotretes</i>	by Jungersen (1911)*
Trebiidae	<i>Saccopsis</i>	by Bresciani & Lützen (1916a)*#
	<i>Trebius</i>	by Gurney (1934)# and Kabata (1979)@
Uncertain ordinal affinity		
Antheacheridae	<i>Mesoglicola</i>	by Taton (1935)*
Uncertain familial affinity		
	<i>Allantogynus</i>	by Changeux (1960)#
	<i>Chordeuma</i>	by Jungersen (1914)#
	<i>Gonophysema</i>	by Bresciani & Lützen (1961b)

Little is known about the leg bearing stages of many highly modified parasites, including internal parasites such as *Aphanodomus* (cf. Bresciani & Lützen, 1974). Furthermore, since only the last nauplius, first copepodid, and adult are known or have been described for *Haplosaccus*, *Haplostoma*, *Graeteriella*, *Speocyclops*, *Bonnerilla*, *Antrocamptus*, *Metis*, *Misophria*, *Cymbasoma*, *Monstrilla*, *Thaumatopsyllus*, *Praecidochondria*, *Pseudacanthocanthopsis*, *Neanthessius*, *Colobomatus*, *Philoblenna*, *Sarcotaces*, *Dissonus*, *Dyspontius*, *Basanistes*, *Clavella*, *Tracheliastes*, *Aspidoecia*, *Choniosphaera*, *Chonistoma*, *Choniorhiza*, *Hansenulus*, *Mysidion*, *Nicothoe*, *Sphaeronellopsis*, and *Allantogynus*, little information can be gleaned about their developmental patterns. In addition some observations are missing

for copepodids of *Gaetanus*, *Euchirella*, *Aetideopsis*, *Calanoides*, *Neocalanus*, *Rhincalanus*, *Heterorhabdus*, *Bathycalanus*, *Megacalanus*, *Gaussia*, *Metridia*, *Scottocalanus*, *Monacilla*, *Ascidicola*, *Enterocola*, *Zancopus*, *Moraria*, *Sunaristes*, *Paratigriopus*, *Miracia*, *Parastenhelia*, *Thalestris*, *Cucumaricola*, *Aspidomolgus*, *Panaietis*, *Paranthessius*, *Ismaila*, *Mesolamproglena*, *Dyspontius*, *Achtheres*, *Clavella*, *Diexanthema*, *Homeoscelis*, *Nicorhiza*, *Sphaeronella*, *Saccopsis*, *Trebius*, *Mesoglicola*, and *Gonophysema*. Missing data for these genera compromise the analysis of developmental patterns in many legs.

Several structures and processes in copepod leg development are defined here. These may be better understood in relation to a common developmental pattern; this coordinated pattern is defined later (see also fig. 2). The first post-maxillipedal leg structure recognized in this study is a primary (1^{\wedge}) leg bud. On a body somite it may be a simple integumental ridge or a rather complex, bilobed or multilobed cuticular structure; by definition here, it bears spines or setae. It is usually the most posterior appendage on the body, and in the following copepodid stage the posterior-most position usually will be taken by the next, new bud on the following body somite. The usual appearance of 1^{\wedge} buds on an animal is described as SERIAL because 1^{\wedge} buds are added anterior-to-posterior to body segments during successive molts (fig. 1).

A 1^{\wedge} bud is usually reorganized during the molt following its initial appearance; the reorganized appendage is more complex, often with 2 basal segments (the proximal is united to its contra-lateral twin by a coupler or interpodal bar); by definition, a reorganized leg possesses an articulated exopod and endopod, each usually 1-segmented. In a partially reorganized leg only one articulated ramus is present; segments of such legs may be described here simply as leg segments without regard to their identification as basipodal, cxopodal, etc. A secondary (2^{\wedge}) leg bud is an unsegmented, dedifferentiated appendage which is derived from a reorganized leg later in development.

	legs					
	1	2	3	4	5	6
N	1^{\wedge} B; 1^{\wedge} B					
I	- ; - ; 1^{\wedge} B					
II	- ; - ; - ; 1^{\wedge} B					
III	- ; - ; - ; - ; 1^{\wedge} B					
IV	- ; - ; - ; - ; - ; 1^{\wedge} B					
V	- ; - ; - ; - ; - ; -					
VI	- ; - ; - ; - ; - ; -					

Fig. 1. Usual appearance of primary leg buds (N = pre-metamorphic nauplius; roman numerals = copepodid stages; 1^{\wedge} B = primary leg bud).

Two kinds of segment additions to rami are recognized here. A SIMULTANEOUS addition occurs when the final, and often homologous, ramal segments are added to legs 1-4 during the same molt. This coordinated addition usually occurs during the molt from the fourth to fifth copepodid (CIV to CV). A simultaneous addition is SUSPENDED when it does not occur during development. Other segment additions are SERIAL and usually occur when non-homologous segments are added to one or more rami during a molt. Rami often undergo serial additions during two successive molts, and usually these additions are not coordinated with additions of homologous segments on other appendages (exceptions include the often coincidental development of legs 1-2). Serial additions derive their name from staggered, anterior-to-posterior changes during successive molts, much like the appearance of 1[^] leg buds. A serial addition is DELAYED when it occurs during a later molt than expected from the defined common pattern, or ACCELERATED when it occurs during an earlier molt than expected; it is SUPPRESSED when it does not occur during development. DOUBLE or TRIPLE additions or reductions occur when two or three segments are added to or deleted from one ramus during a molt.

RESULTS

The presence of a similar pattern for segment development of legs 1-4 in 20 genera (*Calanus*, *Boeckella*, *Centropages*, *Gladioferens*, *Pseudodiaptomus*, *Acanthocyclops*, *Cyclops*, *Eucyclops*, *Notodelphys*, *Pachypygus*, *Pygodelphys* male, *Oithona*, *Nitocra*, *Microsetella*, *Harpacticus*, *Zaus*, *Longipedia*, *Tisbe*, *Midicola*, *Modiolicola*) from 13 families in 4 orders defines a common development pattern in copepod leg ontogeny (fig. 2). In the common pattern, 1[^] buds of post-maxillipedal legs

	legs			
	1	2	3	4
N	1 [^] B;	1 [^] B		
I	1+1;	1+1;	1 [^] B	
II	2+2;	2+2;	1+1;	1 [^] B
III	2+2;	2+2;	2+2;	1+1;
IV	2+2;	2+2;	2+2;	2+2;
V	3+3;	3+3;	3+3;	3+3;
VI	3+3;	3+3;	3+3;	3+3;

Fig. 2. Common pattern of development for legs 1-4 (1+1 = reorganized leg with 1-segmented exopod (Re) and endopod (Ri); 2+2 = leg with 2-segmented exopod and endopod, etc.; remaining legend as for fig. 1).

1-2 first appear together in the naupliar stage prior to metamorphosis to a copepodid. The 1[^] buds of legs 3-4 first appear individually, and in sequence, anterior-to-posterior along the body, on succeeding somites during molts to CI and CII respectively. During the molt following its initial appearance, each 1[^] bud of legs 1-4 undergoes a reorganization. The resulting reorganized appendage, as noted above, has a 1-segmented exopod and 1-segmented endopod. A subsequent serial addition during the molt immediately after reorganization produces a leg with 2-segmented rami.

Further serial additions to both rami of some legs must be suppressed during later molts because in the common pattern (1) legs appear serially anterior-to-posterior along the body in sequence, (2) subsequent molts may add no more than 1 segment to each ramus, and (3) no ramus may have more than 3 segments. Serial additions to legs 1 and 2 (whose initial appearance and subsequent development are coordinated) are suppressed following the molt to CII, while serial additions to leg 3 are suppressed after CIII. In the common pattern, the simultaneous addition of the final, homologous segment to each ramus on legs 1-4 occurs during the molt to CV; each leg attains the adult 3-segmented exopod and endopod. No additional segments are added or lost during the terminal molt to CVI.

Except for missing observations of the pre-metamorphic nauplius, another 11 genera (*Ectocyclops*, *Halicyclops*, *Amphiascoides*, *Amphiascus*, *Robertgurneya*, *Robertsonia*, *Harpacticella*, *Paradactylopodia*, *Benthomisophria*, *Leptinogaster*, and *Ostrincola*), from four more families and one more order, may also exhibit this common pattern. Thus the common pattern may be found among species from 31 genera in 17 families among five of nine orders. In *Macrocyclops* female, *Lernaea*, *Canuella*, *Tigriopus*, and *Scutellidium*, absence of one or both naupliar leg buds is the only exception to the common pattern. From appendages of the remaining 148 genera, 339 individual rami of species in 58 other genera attain a 3-segmented condition by following the pattern of their positional homologues in the common pattern, although the coordinated development of legs 1-4, which is exhibited in the common pattern, is decoupled.

In contrast to the common pattern, legs 1-4 of the following adult copepods may attain 3-segmented rami in ways which differ from their positional homologues in the common pattern:

- Absence of naupliar 1[^] leg buds - *Alteutha* leg 2 exopod and endopod (= Re Ri).
- Delay simultaneous addition - *Mesocyclops* legs 1-4 Re Ri; (fig. 3A).
- Suspension of the simultaneous addition, both serial additions occurring during the last 2 molts - *Euchaeta* male leg 1 Re; *Temora* legs 3-4 Ri; *Platychelipus* female leg 4 Re; *Macrosetella* leg 2 Ri, legs 3-4 Re Ri; (fig. 4A, see legs 3-4 Ri).

	A				B			
	1	2	3	4	1	2	3	4
N	1 [^] B; 1 [^] B				∅	∅		
I	1+1; 1+1; 1 [^] B				1+1	1+1	1 [^] B	
II	2+2; 2+2; 1+1; 1 [^] B				2+2	2+2	1+1	1 [^] B
III	2+2; 2+2; 2+2; 1+1;				2+2; 2+2; 2+2; 1 [^] B;			
IV	2+2; 2+2; 2+2; 2+2;				2+2; 2+2; 2+2; 1+1;			
V	2+2; 2+2; 2+2; 2+2;				2+2; 2+2; 2+2; 1+1;			
VI	3+3; 3+3; 3+3; 3+3;				3+3; 3+3; 3+3; 1+1;			

Fig. 3. A, *Mesocyclops*, legs 1-4; B, *Neoergasilus*, legs 1-4 (legend as for fig. 2).

	A				B			
	1	2	3	4	1	2	3	4
N	1 [^] B; 1 [^] B				1 [^] B; 1 [^] B			
I	1+1; 1+1; 1 [^] B				1+1; 1+1; 1 [^] B			
II	2+1; 2+1; 1+1; 1 [^] B				2+1; 2+2; 1+1; 1 [^] B			
III	2+2; 2+1; 1+1; 1+1;				3+1; 3+2; 2+2; 1+1;			
IV	2+2; 2+1; 1+1; 1+1;				3+1; 3+2; 3+2; 3+2;			
V	3+2; 3+2; 2+2; 2+2;				3+1; 3+2; 3+2; 3+2;			
VI	3+2; 3+2; 3+2; 3+2;				3+1; 3+2; 3+2; 3+2;			

Fig. 4. A, *Temora* legs 1-4; B, *Calamoecia* legs 1-4 (legend as for fig. 2).

- Suspension of simultaneous addition, second serial addition immediately follows first - *Calamoecia* legs 1-3 Re; *Aglaodiaptomus* leg 3 Re; *Diarthrodes* leg 3 Re Ri; (fig. 4B, see Re).
- Suspension of simultaneous addition, second serial addition delayed one molt - *Laophonte setosa* Boeck, 1865 leg 3 Re; *Diarthrodes* leg 2 Re.
- Suspension of simultaneous addition, both serial additions delayed two molts - *Lepeophtheirus* leg 3 Re.
- Suspension of simultaneous addition, both serial additions delayed three molts - *Lepeophtheirus* leg 2 Re Ri.
- Suspension of the simultaneous addition with an extra serial addition during terminal molt - *Acartia clausi* Giesbrecht, 1889 leg 1 Re; *Diacyclops*

- leg 1 Re Ri; *Lamproglena* male leg 1 Re; *Doropygus* legs 3-4 Ri; *Pygodelphys* female legs 2-4 Ri; *Balaenophilus* leg 1 Ri; *Elaphoidella* female leg 1 Ri; *Lep-tastacus* legs 1-4 Re; *Paramphiascella* leg 1 Ri; *Schizopera* leg 1 Ri; *Macrosetella* leg 2 Re; *Euterpina* legs 2-4 Ri; *Tachidius* legs 1-4 Ri; *Trochicola* leg 2 Re; *Ergasilus bryconis* Thatcher, 1981 leg 1 Re, legs 2-3 Re Ri; *Ergasilus lizae* Krøyer, 1863 legs 1-2 Re, leg 3 Ri; *Ergasilus sieboldi* Nordmann, 1832 legs 1-3 Re Ri; *Neoergasilus* legs 1-3 Re Ri; *Thersitina* legs 1-3 Re Ri, leg 4 Ri; (figs. 3B; 5A, see Ri).
- Suspension of simultaneous addition, double serial addition from reorganized leg - *Calamoecia* leg 4 Re; (fig. 4B, see leg 4 Re).
 - Suspension of simultaneous addition, double serial addition from 1[^] leg bud followed by serial addition - *Diarthrodes* leg 4 Re Ri.
 - Suspension of simultaneous addition, double serial addition from 1[^] leg bud delayed one molt - *Cyclopina* legs 1-2 Re Ri; *Laophonte setosa* Boeck, 1865 leg 4 Re.
 - Suspension of simultaneous addition, double serial addition from 1[^] leg bud delayed two molts - *Acartia californiensis* Trinast, 1976 legs 3-4 Re.
 - Suspension of simultaneous addition, double serial addition from 1[^] leg bud delayed three molts - *Acartia californiensis* Trinast, 1976 leg 2 Re; *Laophonte setosa* Boeck, 1865 legs 1-2 Re; *Caligus spinosus* Yamaguti, 1939 leg 2 Ri.
 - Suspension of simultaneous addition, double serial addition from 1[^] leg bud delayed five molts - *Acartia californiensis* Trinast, 1976 leg 1 Re.
 - Suspension of simultaneous addition, accelerated appearance of reorganized leg - *Cyclopina* legs 3-4 Re Ri.
 - Suppression of serial addition, double addition during molt to CV - *Pleuromamma* legs 2-4 Ri; *Paracalanus* legs 2-4 Ri; *Trochicola* male leg 1 Re Ri, leg 2 Ri, legs 3-4 Re Ri; *Oncaea* leg 4 Re; (fig. 5B, see Re).
 - Redevelopment from 2[^] bud - *Haplostomella* male leg 1 Re, legs 2-4 Re Ri; *Enterocola* male legs 1-4 Re Ri; *Sabellacheres* legs 1-2 Re Ri; *Cancerilla* leg 2 Re Ri; (fig. 5C, D).
 - Absence of leg buds at nauplius, double addition (as reorganization plus addition) - *Doroixys* legs 1-2 Re Ri, *Alteutha* leg 1 Re; *Sacodiscus* legs 2-4 Re; (fig. 6A, see Re).
 - Delay 1[^] bud reorganization until CV, double addition - *Sabellacheres* leg 3 Re Ri.
 - Triple addition from 1[^] bud - *Platychelipus* male leg 3 Ri; *Caligus clemensi* Parker & Margolis, 1964 leg 3 Re; *Caligus pageti* Russell, 1925 leg 3 Re.
 - Triple addition from 2[^] bud - *Caligus clemensi* Parker & Margolis, 1964 leg 2 Re Ri.
 - Double addition from 2[^] bud followed by serial addition - *Caligus pageti* Russell, 1925 leg 2 Re Ri.
 - Reduction from 2-segmented to 1-segmented ramus followed by double addition - *Caligus spinosus* Yamaguti, 1939 legs 2-3 Re.

	A	B	C	D
N	-	-	1 [^] B	∅
I	1 [^] B		1+1;	1+1;
II	1+1	1 [^] B;	1+1;	1+1;
III	2+2	1+1;	2 [^] B;	2 [^] B;
IV	2+2	1+2;	1+1;	2 [^] B;
V	3+2	3+3;	2+2;	3+3;
VI	3+3	3+3;	3+3;	3+3;

Fig. 5. A, *Euterpina* leg 3; B, *Oncaea* leg 4; C, *Cancerilla* male leg 2; D, *Caligus* leg 2 (2[^]B = secondary leg bud; remaining legend as for fig. 2).

	A	B	C	D
N	∅	?	1 [^] B	∅
I	2+1;	1+1;	1+1;	2+2;
II	2+2;	2+1;	2+2;	2+2;
III	2+2;	2+2;	2+2;	2+2;
IV	2+2;	2+2;	2+2;	2+2;
V	3+3;	2+2;	3+3;	2+2;
VI	3+3;	2+2;	3+2	2+2;

Fig. 6. A, *Alteutha* leg 1; B, *Taeniacanthus* leg 1; C, *Bryocamptus* male leg 2; D, *Lernaecocera* leg 1 (legend as for fig. 2).

Legs 1-4 of adult copepods may attain 2-segmented rami in the following ways:

- Suspension of simultaneous addition - *Acartia californiensis* Trinast, 1976 legs 3-4 Ri; *Acartia clausi* Giesbrecht, 1889 leg 1 Ri; *Paracartia* leg 1 Ri; *Calamoecia* legs 2-4 Ri; *Diaptomus* leg 1 Ri; *Leptodiptomus* leg 1 Ri; *Skistodiptomus* leg 1 Ri; *Eucalanus* leg 1 Ri; *Xanthocalanus* leg 2 Ri; *Apocyclops* legs 1-4 Re Ri; *Lamproglena* female leg 4 Ri; *Bryocamptus* leg 4 Ri; *Canthocamptus* leg 4 Ri; *Elaphoidella* legs 2-4 Ri; *Cletocamptus* legs 1-4 Ri (except male leg 3 Ri); *Arenopontia* legs 1-4 Ri; *Leptastacus* legs 1-4 Ri; *Laophonte commensalis* Raibaut, 1961 legs 1-4 Ri; *Platychelipus* leg 1 Rc Ri, leg 2 Ri, male leg 4 Ri; *Macrosetella* leg 1 Ri; *Porcellidium* leg 1 Ri; *Euterpina* leg 1 Re Ri;

- Diarthrodes* leg 1 Re; *Tisbintra* leg 1 Ri; *Ergasilus bryconis* Thatcher, 1981 leg 1 Ri; *Sinergasilus* leg 4 Re; *Lichomolgus* leg 4 Ri; *Anchistrotos* leg 1 Re Ri; *Taeniacanthus* leg 1 Re; *Lepeophtheirus* leg 3 Ri; *Cardiodectes* male leg 3 Re; *Lernaocera* leg 2 Re Ri; (fig. 6B, see Re).
- Suspension of simultaneous addition, delay serial addition one molt - *Acartia clausi* Giesbrecht, 1889 leg 4 Ri; *Paracartia* leg 4 Ri; *Ctenocalanus* leg 2 Ri; *Megadiaptomus* leg 1 Ri; *Euchaeta* leg 3 Ri; *Paracalanus* leg 2 Ri; *Calanopia* leg 4 Ri; *Labidocera* leg 4 Ri; *Paralabidocera* leg 4 Ri; *Pontella* leg 4 Ri; *Eurytemora* leg 4 Ri; *Temora* leg 1 Ri, leg 4 Ri; *Tortanus* leg 4 Ri; *Platychelipus* male leg 4 Ri; *Macrosetella* leg 1 Ri; *Ergasilus bryconis* Thatcher, 1981 leg 4 Ri; *Ergasilus sieboldi* Nordmann, 1832 leg 4 Re; *Thersitina* leg 4 Re; *Taeniacanthus* leg 1 Ri; *Lepeophtheirus* leg 3 Ri; (figs. 4A, see leg 1 Ri or leg 4 Ri; 6B).
 - Suspension of simultaneous addition, delay serial addition two molts - *Acartia clausi* Giesbrecht, 1889 leg 3 Ri; *Paracartia* leg 3 Ri; *Bradyidius* leg 2 Ri; *Aglaodiaptomus* leg 1 Ri; *Calanopia* leg 3 Ri; *Labidocera* leg 3 Ri; *Paralabidocera* leg 3 Ri; *Pontella* leg 3 Ri; *Eurytemora* leg 3 Ri; *Temora* leg 3 Ri; *Tortanus* leg 3 Ri; *Macrosetella* male leg 3 Ri; *Ergasilus bryconis* Thatcher, 1981 leg 4 Re; *Ergasilus lizae* Krøyer, 1863 leg 4 Re; *Caligus pageti* Russell, 1925 leg 1 Re; *Lepeophtheirus* leg 1 Re; *Cardiodectes* legs 1-2 Re Ri; (fig. 4A, see leg 3 Ri).
 - Suspension of simultaneous addition, delay serial addition three molts - *Acartia clausi* Giesbrecht, 1889 leg 2 Ri; *Paracartia* leg 2 Ri; *Euchaeta* leg 1 Re; *Paracalanus* leg 1 Ri; *Calanopia* legs 1-2 Ri; *Labidocera* legs 1-2 Ri; *Paralabidocera* leg 2 Ri; *Pontella* leg 2 Ri; *Eurytemora* leg 2 Ri; *Temora* leg 2 Ri; *Tortanus* leg 2 Ri; *Balaenophilus* leg 2 Ri; *Cancerilla* male leg 1 Ri; (figs. 4A, see leg 2 Ri; 7A, see Ri).
 - Reduction during terminal molt - *Lamproglena* female legs 1-3 Re Ri, leg 4 Re; *Bryocamptus* male leg 2 Ri; *Cletocamptus* male leg 3 Ri; *Parastenhelia* leg 1 Ri; *Diarthrodes* leg 2 Ri; *Lamproglena chinensis* Yu, 1937 female legs 1-4 Re Ri; (fig. 6C, see Ri).
 - Double serial addition during reorganization and suppression of later serial additions - *Acartia californiensis* Trinast, 1976 legs 1-2 Ri; *Laophonte setosa* Boeck, 1865 legs 1-2, 4 Ri; *Caligus clemensi* Parker & Margolis, 1964 leg 3 Ri; *Caligus pageti* Russell, 1925 leg 3 Ri; *Lernaenicus* legs 3-4 Re; *Lernaocera* leg 1 Re Ri; (fig. 6D see Ri).
 - Redevelopment from 2[^] bud - *Haplostomella* male leg 1 Ri; *Caligus clemensi* Parker & Margolis, 1964 leg 1 Re.
 - Reduction from 2-segmented to 1-segmented ramus followed by serial addition - *Caligus spinosus* Yamaguti, 1939 leg 1 Re.

Legs 1-4 of adult copepods may attain 1-segmented rami in the following ways:

- Suppression of serial addition and suspension of simultaneous addition -

	A	B		C	D
		2	3		
N	1 [^] B	∅	-	-	-
I	1+1;	1+1; 1 [^] B;		-	-
II	2+1;	1+1; 1 [^] B;		1 [^] B	1 [^] B
III	2+1;	1+1; 1 [^] B;		1+∅;	1+1;
IV	2+1;	1+1; 1+1;		1+∅;	2+2;
V	3+2;	1+1; 1+1;		2+∅;	3+2;
VI	3+2;	1+1; 1+1;		3+1;	3+1;

Fig. 7. A, *Labidocera* leg 2; B, *Trochicola* legs 2, 3; C, *Platychelipus* female leg 4; D, *Elaphoidella* leg 4 (legend as for fig. 2).

Bradyidius leg 1 Ri; *Chiridius* leg 1 Ri; *Calamoecia* leg 1 Ri; *Clausocalanus* leg 1 Ri; *Ctenocalanus* leg 1 Ri; *Euchaeta* legs 1-2 Ri; *Xanthocalanus* leg 1 Ri; *Epischura* legs 1-4 Ri; *Eurytemora* leg 1 Ri; *Heterocope* legs 1-4 Ri; *Balaenophilus* legs 3-4 Ri; *Corycaeus* leg 4 Ri; *Mytilicola* legs 1-2 Re Ri; *Trochicola* female legs 1-2 Re Ri (legs 1-2 do not begin as buds); *Cancerilla* legs 1-2 Re Ri; *Lernanthropus* legs 1-2 Re Ri; (fig. 7B, see leg 2).

- Reorganization of 1[^] bud delayed, suppression of serial addition and suspension of simultaneous addition - *Neoergasilus* leg 4 Re Ri; *Mytilicola* legs 3-4 Re Ri; *Trochicola* legs 3-4 Re Ri; (figs. 3B, see leg 4; 7B, see leg 3).
- Late redevelopment from 2[^] bud - *Enterocola* female legs 1-4 Re Ri.
- Partial reorganization of leg, development of one ramus delayed until terminal molt - *Platychelipus* female leg 4 Ri; (fig. 7C, see Ri).
- Early loss of ramus followed by redevelopment - *Caligus spinosus* Yamaguti, 1939 leg 1 Ri; *Lepeophtheirus pectoralis* (Müller, 1776) leg 1 Ri.
- Suspension of simultaneous addition and reduction in segment number - *Elaphoidella* male leg 4 Ri; *Caligus spinosus* Yamaguti, 1939 leg 3 Ri; (fig. 7D, see Ri).

Legs 1-4 of adult copepods also may be made up of a multiple or single segmented ramus (as a partially reorganized leg), a 2[^] bud, a 1[^] bud, or one or more legs may be absent. A multiple or single segmented ramus is attained by:

- Partial reorganization of 1[^] leg bud to a single segment followed by one or more serial additions - *Caligus* leg 4 Re; *Lepeophtheirus* leg 4 Re; *Cardiodectes* leg 3; *Lernaenicus* legs 3-4; *Lernaecocera* legs 3-4; *Sarcotretes* leg 3.

- Partial reorganization of 1[^] leg bud to a single segment during molt to CVI - *Sabellacheres* leg 4.
- Loss of ramus from reorganized leg - *Caligus* leg 1 Ri; *Lepeophtheirus* leg 1 Ri.

2[^] buds are attained by:

- Reduction from a reorganized leg with 2-segmented rami through 1-segmented rami to 2[^] bud - *Enteropsis* female legs 1-2; *Scolecodes* female legs 1-2; (fig. 8A).
- Reduction from a reorganized leg with 1-segmented rami to 2[^] bud - *Enteropsis* female leg 3; *Scolecodes* female legs 3-4; *Acanthochondria* legs 1-2; *Diexanthema* male legs 1-2; *Chordeuma* legs 1-4; (fig. 8A).

	A				B			
	1	2	3	4	1	2	3	4
N	1 [^] B;	1 [^] B			1 [^] B;	1 [^] B		
I	1+1;	1+1;	1 [^] B		1+1;	1+1;	1 [^] B	
II	2+2;	2+2;	1+1;	1 [^] B	2+2;	2+2;	1+1;	1 [^] B
III	1+1;	1+1;	1+1;	1 [^] B;	1+1;	1+1;	1+1;	1 [^] B;
IV	1+1;	1+1;	1+1;	1+1;	1+1;	1+1;	1+1;	1+1;
V	1+1;	1+1;	1+1;	1+1;	3+3;	3+3;	3+3;	3+3;
VI	2 [^] B;	2 [^] B;	2 [^] B;	2 [^] B;	3+3;	3+3;	3+3;	3+3;

Fig. 8. *Scolecodes*. A, female legs 1-4; B, male legs 1-4 (legend as for fig. 5).

- Initial serial addition to reorganized leg followed by a double reduction from leg with 2-segmented rami - *Salmincola* males legs 1-2.
- Formation of 2[^] bud from reorganized leg; development of 1-segmented ramus from 2[^] bud followed by subsequent redevelopment back to 2[^] bud - *Haplostomella* legs 1-4 Ri.

By definition 1[^] buds are attained by:

- No further development of 1[^] bud - *Enteropsis* female leg 4; *Cancerilla* leg 3; *Diexanthema* male legs 3-4; *Cardiodectes* leg 4.

Leg absence is attained by:

- 1[^] bud does not appear during development - *Cancerilla* leg 4; *Alella* leg 4; *Salmincola* leg 4; *Lernanthropus* leg 4; *Diexanthema* female leg 4.

- Loss of 1[^] bud - *Acanthochondria cornuta* Müller, 1776 legs 3-4; *Acanthochondria yui* Shiino, 1964 leg 3; *Alella* leg 3; *Salmincola* leg 3; *Lernanthropus* leg 3; *Diexanthema* female leg 3.
- Formation of 2[^] bud from reorganized leg, followed by loss of 2[^] bud - *Alella* legs 1-2; *Vanbenedenia* legs 1-2; *Diexanthema* female legs 1-2.
- Serial addition to reorganized leg produces 2-segmented rami, formation of 2[^] bud, followed by loss of 2[^] bud - *Salmincola* female legs 1-2.

Leg 5 development in gymnopleans does not fit the common pattern because segments are added during the terminal molt, and asymmetrical segment numbers in leg 5 are common among adult calanoid males. In *Calanus* males and females, leg 5 development fits most closely the common pattern for legs 1-4. The 1[^] bud of CIII is reorganized, 2 serial single additions follow, producing 3-segmented rami; the last segment is gained during the terminal molt (fig. 9A). Females of *Boeckella*, *Centropages*, and *Gladioferens* also follow this pattern, while in *Undinula* and *Bathycalanus* the reorganized leg has been reported during CIII, and after a 1 molt delay, all subsequent additions follow the *Calanus* pattern.

In males of many calanoid genera, a partial reorganization of the 1[^] bud of leg 5 occurs and only the exopod is present. *Heterocope* male Ri is the only appendage in which a ramus (1-segmented) is present in CV but lost during the terminal molt.

In gymnoplean leg 5, a 3-segmented ramus may develop by:

- Two serial additions after reorganization - *Acartia californiensis* Trinast, 1976 male Re; *Bradyidius* male Re; *Boeckella* male Re; *Gladioferens* male Re; *Clausocalanus* male Re; *Ctenocalanus* male Re; *Megadiaptomus* female Re; *Gaussia* Re; *Metridia* male Re; *Pleuromamma* male Re (Re1 is fused to the basipod in this genus); *Paracalanus* male Re; *Xanthocalanus* male Re.
- Double addition during reorganization - *Calamoecia* male Re; (fig. 9B, see Re).
- Double addition from CIV to CV - *Chiridius* male Re; *Gaetanus* male Re; *Euchirella* male Re; *Calamoecia* male Ri; *Euchaeta* male Re; *Labidocera* male Re; (fig. 9B, see Ri).
- Double addition from CV to CVI - *Boeckella* male Re.

2-segmented rami occur by:

- Suppression of the first serial addition (CIV to CV) - *Chiridius* male Re; *Gaetanus* male Re; *Euchirella* male Re; *Rhincalanus* male Ri; *Calanopia* female Re; *Labidocera* male Re; *Paralabidocera* male Re; *Pontella* male Re; *Pseudodiaptomus* female Re; *Eurytemora* male Re; *Temora* male Re; *Tortanus* male Re.
- Suppression of the second serial addition (during CV to CVI) - *Acartia clausi* Giesbrecht, 1889 male Re; *Paracartia* male Re; *Boeckella* male Re Ri; *Cen-*

	A	B
N	-	-
I	-	-
II	-	-
III	1 [^] B	1 [^] B
IV	1+1;	2+1;
V	2+2;	3+1;
VI	3+3;	3+3;

Fig. 9. A, *Calanus* leg 5; B, *Calamoecia* male leg 5 left (legend as for fig. 2).

tropages male Re; *Gladioferens* male Re Ri; *Aglaodiaptomus* Re; *Diaptomus* Re; *Leptodiaptomus* Re; *Megadiaptomus* male Re; *Skistodiaptomus* Re; *Eucalanus* male Re; *Metridia* male Re; *Pleuromamma* female Re; *Pseudodiaptomus* male Re; *Epischura* Re; *Eurytemora* female Re; *Heterocope* Re.

1-segmented rami occur by:

- Suppression of both serial additions - *Acartia clausi* Giesbrecht, 1889 male Re; *Paracartia* male Re; *Bradyidius* male Ri; *Chiridius* male Ri; *Gaetanus* male Ri; *Euchirella* male Ri; *Calamoecia* male Ri; *Clausocalanus* Re; *Aglaodiaptomus* Ri; *Diaptomus* Ri; *Leptodiaptomus* Ri; *Megadiaptomus* male Ri; *Skistodiaptomus* Ri; *Rhincalanus* male Re; *Euchaeta* male Ri; *Xanthocalanus* female Re; *Calanopia* male Re; *Labidocera* female Re Ri; *Paralabidocera* female Re Ri; *Pontella* female Re Ri; *Temora* female Re; *Tortanus* Re.
- Development of ramus delayed until terminal molt - *Paracartia* male Ri.

The following are unusual developmental patterns in leg 5 of gymnopleans: partial reorganization from 1[^] bud to produce 1-segmented leg with 2 basal elements, and no further change - *Acartia* female, *Rhincalanus* female, *Paracalanus* female; ramus absent by suppression of first serial addition and loss of segment - *Ctenocalanus* male; bud reorganization delayed 1 molt, reorganization producing a 2-segmented ramus, and suppression of last serial addition - *Pseudodiaptomus* male; double addition during leg reorganization - *Calamoecia* male Re.

In adult calanoid females without fifth legs (e.g. most amphascandrians), the 1[^] bud of leg 5 usually does not appear during development. The plate covering the gymnoplean female genital opening has been considered a fused leg 6 (Von Vaupel Klein, 1982). However, this plate appears during the terminal molt, and there are no reports of a 1[^] bud of leg 6 in prior stages. Furthermore,

the initial appearance of leg 6 at CVI is unusual among podoplean copepods (only 6 genera). The appearance of this gymnoplean plate may not be part of a coordinated leg development system.

Among podopleans, *Sacodiscus* male leg 5 undergoes a partial reorganization to a leg with 2-segments at CIV; this leg is completely reorganized with 1-segmented exopod and endopod during the terminal molt. This is the only genus for which complete development of a reorganized podoplean leg 5 is known. In *Metis* adult males and *Lamproglena carassii* Sproston, Yin & Yu, 1950 adult females, leg 5 eventually is reorganized from the 1[^] bud stage; the reorganized leg, with two 1-segmented rami, is present in CVI but its structure in earlier stages is unknown. *Longipedia* leg 5 is reorganized at CIV (immediately after 1[^] bud) with two 1-segmented rami, but the endopod is lost during the terminal molt.

A partially reorganized podoplean leg 5 may occur in several ways. A 3-segmented leg 5 may develop by partial reorganization of a 1[^] bud during the molt to CVI - *Parastenhelia* male.

A 2-segmented leg 5 may develop by:

- 1[^] bud absent, partial reorganized leg appears during CIII with subsequent serial additions suppressed - *Macrocylops*.
- Partial reorganization from 1[^] bud to 2-segmented leg - *Sacodiscus* female.
- Partial reorganization to a 1-segmented leg with one subsequent serial addition - *Leptinogaster*, *Ostrincola*, *Anchistrotos*, and *Taeniacanthus*.

A 1-segmented leg 5 may develop by:

- Partial reorganization to a 1-segmented leg from CIII to CIV with all subsequent serial additions suppressed - *Acanthocylops*, *Cyclops*, *Diacyclops*, *Ectocylops*, *Halicyclops*, *Mesocylops*, *Lernaea*, *Pachypygus*, *Nitocra*, *Harpacticella* male, *Paratigriopus* female, *Zaus* male, *Diarthrodes*, *Tisbe*, *Tisbintra*, *Benthomisophria*, *Lichomolgus*, *Midicola*, *Modiolicola*.
- 1[^] bud absent at CIII but partially reorganized leg present at CIV with all subsequent serial additions suppressed - *Macrosetella*.
- Partial reorganization to a 1-segmented leg delayed one molt to CV, with subsequent serial addition suppressed - *Doropygus*, *Notodelphys*, *Scolecodes* male, *Oithona*, *Microsetella*, *Harpacticus* male, *Paratigriopus* male, *Tigriopus*, *Zaus* female, *Alteutha*, *Scutellidium*, *Aspidomolgus*, *Oncaea* female, *Cancerilla* male.
- Partial reorganization to a 1-segmented leg delayed 2 molts to CIV - *Apocylops* female, *Cyclopina*, *Bryocamptus*, *Canthocamptus*, *Elaphoidella*, *Amphiascoides*, *Amphiascus*, *Paramphiascella*, *Robertgurneya*, *Robertsonia*, *Schizopera*, *Laophonte commensalis* Raibaut, 1961, *Platychelipus* female, *Porcellidium*, *Euterpina* female, *Paradactylopodia*, *Eudactylopus* female.

Leg 5 may remain a 1[^] bud (with all serial additions suppressed) initially appearing at:

- CII - *Lamproglena chinensis* Yu, 1937, *Sunaristes*.
 CIII - *Apocyclops* male, *Pygodelphys*, *Scolecodes* female; *Canuella*, *Cletocamptus*, *Arenopontia*, *Harpacticus* female, *Platychelipus* male, *Euterpina* male, *Tachidius*, *Eudactylopus* male, *Corycaeus*, *Ergasilus*, *Neoergasilus* female, *Sinergasilus*, *Thersitina*, *Oncaea* male, *Caligus pageti* Ben Hassine, 1983, *Lepeophtheirus* (both as *chalmus* 1), and *Cancerilla* female.
 CIV - *Haplostomella*, *Eucyclops*, *Doroixys*, *Balaenophilus*, and *Trochicola*.
 CV - *Leptastacus*, *Laophonte setosa* Boeck, 1865, *Mytilicola*, *Caligus clemensi* Parker & Margolis, 1964, and *Caligus spinosus* Yamaguti, 1939 (both as preadult).
 CVI - *Cymbasoma* female and *Monstrilla*.

Leg 5 has not been reported during development of *Enteropsis* female, *Cymbasoma* male, *Acanthochondria*, *Neoergasilus* male, *Sabellacheres*, *Alella*, *Salmincola*, *Vanbenedenia*, *Lernanthropus*, *Cardiodectes*, *Lernaenicus*, *Sarcotretes*, and *Chordeuma*.

Among podopleans leg 6 remains a 1[^] bud; it may first appear at:

- CIII - *Lamproglena chinensis* Yu, 1937.
 CIV - *Haplostomella*, *Acanthocyclops*, *Apocyclops*, *Cyclops*, *Diacyclops*, *Ectocyclops*, *Halicyclops*, *Mesocyclops*, *Lernaea*, *Doropygus*, *Notodelphys*, *Pachypygus*, *Pygodelphys*, *Scolecodes*, *Oithona*, *Nitocra*, *Balaenophilus*, *Bryocamptus*, *Canthocamptus*, *Canuella*, *Cletocamptus*, *Arenopontia*, *Amphiascoides*, *Amphiascella*, *Paramphiascella*, *Robertgurneya*, *Robertsonia*, *Schizopera*, *Microsetella*, *Harpacticella*, *Harpacticus*, *Laophonte commensalis*, Raibaut, 1961, *Platychelipus* female, *Longipedia*, *Sacodiscus* male, *Euterpina* male, *Tachidius*, *Eudactylopus* male, *Tisbe*, *Tisbintra* male, *Benthomisophria*, *Leptinogaster*, *Corycaeus*, *Ergasilus* male, *Sabellacheres*, *Aspidomolgus*, *Lichomolgus*, *Ostrincola*, *Midicola*, *Modiolicola*, *Paranthesius*, *Lepeophtheirus* male (*chalmus* 5), *Cancerilla*.
 CV - *Eucyclops*, *Macroscyclops*, *Elaphoidella*, *Tigriopus*, *Macrosetella*, *Eudactylopus* female, *Acanthochondria yui* Shiino, 1964, *Oncaea*, *Caligus clemensi* Parker & Margolis, 1964, *Caligus spinosus* Yamaguti, 1939 (both as preadult).
 CVI - *Cyclopina* male, *Leptastacus*, *Laophonte setosa* Boeck, 1865, *Paratigriopus*, *Zaus*, *Platychelipus* male, *Diarthrodes*, *Cymbasoma*, *Monstrilla*, and *Thersitina*.

Leg 6 has not been reported during development of *Enteropsis* female, *Cyclopina* female, *Sunaristes*, *Alteutha*, *Euterpina* female, *Paradactylopodia*, *Porcellidium*, *Scutellidium*, *Tisbintra* female, *Acanthochondria cornuta* Müller, 1776, *Ergasilus* female, *Neoergasilus*, *Sinergasilus*, *Mytilicola*, *Trochicola*, *Taeniacanthus*, *Caligus* female, *Lepeophtheirus* female, *Alella*, *Salmincola*, *Vanbenedenia*, *Lernanthropus*, *Diexanthema*, *Cardiodectes*, *Lernaenicus*, *Lernaecera*, *Sarcotretes*, and *Chordeuma*.

Several generalities about development of post-maxillipedal legs emerge from this survey:

- Rami are never more than 3-segmented (and legs never more than 5-segmented including two basal segments) although it appears possible to develop a 4-segmented ramus (see *Serpuliphilus tenax* Humes & Stock, 1973 in Humes & Stock 1973, and *Euchirella messinensis* (Claus, 1863) in Von Vaupel Klein, 1984).
- With the exceptions of *Acartia californiensis* Trinast, 1976, *Calamoecia*, *Aglaodiptomus*, *Macrocylops* male, *Cyclopina*, *Laophonte setosa* Boeck, 1865, *Porcellidium*, *Diarthrodes*, and *Caligus*, 3-segmented rami usually do not appear earlier than CV; *Calamoecia* legs 1-2 Re and *Cyclopina* legs 1-3 Re Ri are the only rami with three segments at CIII.
- The simultaneous addition, when legs 1-4 together gain their final segments during the same molt, occurs during the molt to CV in 59 genera; in 51 genera these segments are homologous and in 50 genera the homologous segment added is the third. Similarly coordinated additions occur in *Mesocyclops*, *Scolecodes* female and *Sabellacheres* which gain final (but not necessarily third) segments during the molt to CVI.
- During a molt, more than one segment seldom is added to a ramus.
- Rami of less than three segments usually result from suppression of serial additions and/or suspension of the simultaneous addition; in contrast, reductions in segment numbers during development are found in 18 genera from 5 orders - *Heterocope*, *Enteropsis*, *Haplostomella*, *Lamproglena*, *Scolecodes*, *Bryocamptus*, *Elaphoidella*, *Cletocamptus*, *Longipedia*, *Parastenhalia*, *Diarthrodes*, *Acanthochondria*, *Caligus*, *Lernanthropus*, *Alella*, *Salmincola*, *Sarcotretes*, and *Chordeuma*.
- Metamorphosis from a free-swimming nauplius produces a predictable leg pattern in the immediate post-metamorphic copepodid of most genera; legs 1-2 are reorganized with 1-segmented rami, and leg 3 appears as a 1[^] bud. Exceptions to this pattern in which a greater number and/or more complex legs are present in the immediate post-metamorphic copepodid include species from 20 genera in 5 orders - *Acartia californiensis* Trinast, 1976, *Skistodiptomus*, *Xanthocalanus*, *Haplostomella*, *Entericola*, *Cyclopina*, *Bonnierilla*, *Doroixys*, *Arenopontia*, *Laophonte setosa* Boeck, 1865, *Platychelipus*, *Macrosetella*, *Alteutha*, *Sacodiscus*, *Thalestris*, *Cymbasoma*, *Monstrilla*, *Cucumaricola*, *Oncaea*, and *Lernaeocera*. The genera *Hansenulus*, *Salmincola* and *Nicthoe* are exceptions because no free nauplius has been reported.
- Development of the gymnoplean genital plate and copepod caudal ramus (present in all copepodid stages) seems to lie outside the leg bud system; leg 6 is common among podopleans but absent in gymnopleans.
- During development from 1[^] leg bud, reorganized legs 1-4 usually have a 1-segmented exopod and endopod. Genera in which a reorganized leg initially has rami with more than one segment include - *Acartia californiensis*

Trinast, 1976, *Xanthocalanus*, *Haplostomella*, *Entericola*, *Cyclopina*, *Bonnierilla*, *Doroixys*, *Arenopontia*, *Laophonte setosa* Boeck, 1865, *Platychelipus*, *Alteutha*, *Sacodiscus*, *Oncaea*, *Lernaenicus*, and *Lernaecocera*.

DISCUSSION

These data suggest that similar adult segment numbers resulting from different developmental patterns are common among copepod post-maxillipedal legs; e.g., there are 23 different patterns which produce an adult leg with 3-segmented rami in addition to the common pattern. Some of these convergences may be unique; e.g., although a coordinated addition of final, homologous, third segments on legs 1-4 occurs during the molt to CV among 31 genera in 17 families that exhibit the common pattern plus *Undinula*, *Bathycalanus*, *Megacalanus*, *Gaussia*, *Metridia*, *Pleuromamma*, *Macrocylops* female, *Lernaea*, *Scolecodes* male, *Canuella*, *Sunaristes*, *Paratigriopus*, *Tigriopus*, *Parastenhelia*, *Alteutha*, *Sacodiscus*, *Scutellidium*, *Trochicola* male, *Oncaea*, and *Paranthesius* (51 taxa in all); similar coordinated additions of homologous, third segments during the molt to CVI are known only in *Mesocylops*.

Differing developmental patterns which lead to convergence in adult structures also can be identified for 2-segmented and 1-segmented rami on legs 1-4, and in the relatively simpler legs 5-6. For example, leg 6 is never reorganized from a 1st bud and most commonly appears initially at CIV. However, an initial appearance at CV occurs in two cyclopoids, four harpacticoids, two poecilostomatoids, and a siphonostomatoid. Although leg 5 may be partially or incompletely reorganized, in many genera it remains a 1st bud and usually appears initially at CIII. It has been reported at CII in a cyclopoid and harpacticoid, while in three cyclopoids (including two confamilials), a harpacticoid, and a poecilostomatoid, it initially appears at CIV.

In families where complete development of four or more genera is known and where setal numbers allow a more careful analysis of homologies (Centropagidae (4 genera), Diaptomidae (5), Pontellidae (4), Temoridae (5), Cyclopidae (10), Notodelphyidae (5), Diosaccidae (5), Harpacticidae (4), and Ergasilidae (4) patterns of development often are uniform through the family. However, genera exhibiting convergent development are known in some of these families. Here again analyses of legs 1-4 with 3-segmented rami are instructive. Development of 3-segmented rami within diaptomids, pontellids, harpacticids and diosaccids is relatively uniform, and usually follows the common pattern (leg 1 endopod of diaptomids is 2-segmented and 2-segmented endopods of pontellids contrast in their development) although leg 1 endopod of *Paramphiascella* and *Schizopera* gains its final, third segment during molt to CVI.

Adult centropagids have 3-segmented rami on legs 1-4 in *Boeckella*, *Centropages*, and *Gladioferens*, and their development follows the common pattern.

In *Calamoecia* (fig. 4B) the exopods of legs 1-4 are also 3-segmented but in no case are the developmental patterns (which include attainment of 3-segmented exopods at CIII or CIV) similar to their positional homologues among the other confamilial genera. In three tcmorid genera development of 3-segmented exopods on legs 1-4 follows their positional homologues in the common pattern. Exopods of legs 3-4 in *Temora* (fig. 4A) are also 3-segmented, but again their developmental patterns (including attainment of 3-segmented exopods at CIV) differ from their positional homologues in the other genera.

Among adult cyclopids all rami are 2-segmented in *Apocyclops*, *Graeteriella*, and *Speocyclops*, and 3-segmented in *Acanthocyclops*, *Cyclops*, *Diacyclops*, *Ectocyclops*, *Eucyclops*, *Halicyclops*, *Macroscyclops*, and *Mesocyclops*. Most rami of the latter eight exhibit developmental patterns similar to those of positional homologues in the common pattern (exceptions are *Diacyclops* leg 1 and *Macroscyclops* male leg 3). All rami of *Mesocyclops* (fig. 3A) differ markedly because the simultaneous addition occurs between CV and CVI, not CIV and CV as in the common pattern. Adult notodelphyids of the genera *Notodelphys*, *Pachypygus*, and males of *Pododelphys* have three segments on both rami of legs 1-4; development follows the common pattern. Both rami of legs 1-2 of *Doropygus* and leg 1 plus the exopods of legs 2-4 of *Pygodelphys* females also follow their positional homologues in the common pattern, while the remaining endopods (on legs 3-4 of *Doropygus* and 2-4 of *Pygodelphys*) add their final segment during the terminal adult molt. Development of *Scolecodes* is quite different from the other three notodelphyid genera; legs 1-4 of adult female *Scolecodes* are 2⁺ buds attained at CVI (fig. 8A), while those of the males (fig. 8B) have 3-segmented rami which develop by adding two segments during the molt to CV, in effect double simultaneous additions. Finally, in three ergasilid genera (*Ergasilus*, *Neoergasilus*, and *Thersitina*), the third segment on both rami of legs 1-3 is gained during the terminal molt, while in *Sinergasilus* this segment is gained at CV.

Copepod post-maxillipedal legs suggest homeotic structures in their sequence of appearance and development (figs. 1-2). Initially these appendages appear along the antero-posterior axis as linearly repeated structures associated with body segmentation, they share a common, early pattern of development, and they exist in several, distinct, final character states on the same organism. A survey of homeotic structures among animal phyla is presented by Ouweneel (1976). Embryology and genetics of tagmosis in *Drosophila melanogaster*, a well-studied system of homeotic structures, has been summarized by Lewis (1963, 1978, 1981, and 1982). Recent data on molecular genetics of gene systems controlling *Drosophila* development are presented by Bender et al. (1983) and Scott et al. (1983). Much of this information about homeotic gene systems has been applied to an explanation of fruit fly development. However, control of these systems during development also has implica-

tions in resolving of transformation series in phylogenetic analyses. Hypotheses outlining the control of tagmosis in the fly may be instructive for arthropod phylogenetics, and these may have particular value for interpretation of reduction sequences such as segmentation patterns in copepod legs.

There are two models for control of somite differentiation during fruit fly development (Duncan & Lewis, 1982; Lawrence & Morata, 1983), but both have several aspects in common. Briefly, in each developing cell a single set of two gene complexes, Antennapedia and Bithorax, controls the developmental pattern of most body somites in the fly. Thus the genome of each fly cell does not carry an individual gene complex for every segment (i.e. one complex for thorax 1, a second for thorax 2, a third for thorax 3, etc.). Rather a single complex, Antennapedia, controls tagmosis of the head and thorax 1, and a second, Bithorax, controls thorax 2 through abdomen 7 (the terminal abdominal somite lies outside the control of the two major complexes). The developmental fate of each somite is effected by the degree to which various structural genes or their modifying genes within each complex have affinities for several repressor substances which block gene function. Variations in repressor substances may be mediated by anterior-to-posterior concentration gradients along the embryo (Duncan & Lewis, 1982) or by positional relationships of cell polyclones early in embryogenesis (Lawrence & Morata, 1983).

While many aspects of these hypotheses remain to be tested in *Drosophila*, the basic implications for evolutionary transformations such as reduction sequences of ramal segments in copepods may best be understood by considering phylogenetic inferences which can be drawn from the phenotype expressed by homeotic and non-homeotic modes of development. If copepod leg development is not homeotic, and the development of each leg is controlled by its own discrete segment of the genome, two possible inferences can be drawn about descendant phenotypes of an adult with, e.g., 1-segmented rami on leg 1 and 3-segmented rami on legs 2-4:

(1) Part of the genome controlling development of a 2nd or 3rd segment on leg 1 is lost. In this case descendants will never develop 2- or 3-segmented rami on leg 1. Or:

(2) Part of the genome controlling development of a 2nd or 3rd segment on leg 1 is repressed. In this case it is possible that descendants could develop 2- or 3-segmented rami on leg 1 if the affinity for repressor substances at the site of the gene system controlling that particular leg were altered.

If development is controlled by a homeotic gene system, gene repression can not be eliminated as the cause of segment reductions, and inferences about point #2 also are affected by the present structure of legs 2-4, as well as leg 1. Because the phenotypes of all legs are the product of actions of the same gene complex, as long as 3-segmented rami exist on at least one leg, an adult copepod could still give rise to a descendant with 3-segmented rami on all legs. In the example above, presence of 3-segmented rami on legs 2-4 would indicate

that the homeotic gene complex controlling leg development still is capable of producing 3-segmented rami on leg 1, if gene repression can be altered. It follows that, given an adult copepod with 3-segmented rami on legs 1-4, it is difficult to eliminate as its ancestor a copepod with a 3-segmented ramus on leg 1 and legs 2-4 absent. Homeotic development also provides a satisfactory alternative to the teleological complications of Soto. Copepods with fewer leg segment numbers that result from repression of a single homeotic gene complex still may give rise to descendants with greater numbers of segments through alterations in the affinity for repressor substances at specific gene sites.

SUGGESTIONS

While numerous developmental convergences in structure suggest that simple loss or gain of repeating structures may be an easily-effected, evolutionary transformation, recognition of these differing developmental patterns may permit definition of a greater number of character states than simple comparisons of adult structural patterns alone. To be used successfully in replacing analyses of adult character states, a common nomenclature for developmental patterns and common method of application should be agreed upon. Nomenclature and methods will be more powerful if they can be applied to all developing appendages, not simply post-maxillipedal legs as has been done here. Basic markers, such as stages at which an appendage first appears and at which the adult condition is attained, may facilitate establishment of developmental homologies. Continued scrutiny of known patterns, including extent of polymorphism and discovery of new ones in other genera will provide better information for analysis.

Reductions of segment numbers during development, while uncommon, appear among copepods in five orders. Presence of these patterns and unusual 4-segmented rami reported by Humes & Stock (1973) and Von Vaupel Klein (1984) suggest that molecular repressing systems in genetic mechanisms may be expected during development of copepod legs. Furthermore, if a homeotic gene system controls this development, greater caution will have to be exercised in eliminating various possible ancestral character states and conclusively establishing transformation series, as noted above.

Finally, discovery of a well-defined, common pattern of development (fig. 2) which appears coordinated among legs 1-4, and present in 31 genera from 17 families among five orders, strengthens the hypothesis of Boxshall et al. (1984) that 3-segmented rami represent the primitive leg condition among copepods. There is no widespread alternate pattern of development, coordinated among more than two legs, which results in an adult with legs of less than three ramal segments. However, many developmental patterns produce 2-segmented rami before CV. The existence of the common pattern should not preclude discussion of a copepod ancestor (fig. 10) with legs of 2-segmented

	legs					
	1	2	3	4	5	6
preN	1 [^] B;					
N	1+1;	1 [^] B				
I	2+2;	1+1;	1 [^] B			
II	2+2;	2+2;	1+1;	1 [^] B		
III	2+2;	2+2;	2+2;	1+1;	1 [^] B	
IV	2+2;	2+2;	2+2;	2+2;	1+1;	1 [^] B
V	2+2;	2+2;	2+2;	2+2;	2+2;	1 [^] B
VI	2+2;	2+2;	2+2;	2+2;	2+2;	1 [^] B

Fig. 10. Alternate pattern of development of legs 1-6 in an ancestral copepod (preN = naupliar stage prior to pre-metamorphic nauplius; remaining legend as for fig. 2).

rami that developed from 1[^] buds, became reorganized, and underwent only one subsequent serial addition: a pattern similar to development of legs 2-4 in *Apocyclops*. In this decoupled hypothesis, the coincidental development of legs 1-2 and simultaneous addition of a third segment on legs 1-4 would have evolved subsequently within the Copepoda, perhaps more than once.

ACKNOWLEDGEMENTS

Special thanks are due to the late Charles Branch Wilson without whose library a topic of this complexity could not have been undertaken, and to T. C. Walter, present keeper of the Wilson Library. K. Preslock, Smithsonian Institution's librarian at the Museum Support Center, provided untiring assistance in obtaining articles not in the Wilson Library. J. Bishop-Rayle (George Mason University) collected specimens of *Mesocyclops* for examination. H. Björnberg (Universidade de São Paulo), A. Campaner (Universidade de São Paulo), A. Humes (Boston University), and W. Vervoort (Rijksmuseum van Natuurlijke Historie, Leiden), checked drafts of table I and offered many suggestions and corrections. J. Reid (Smithsonian Institution), provided corrections to diaptomid and cyclopid genera. O. Ben Hassine (Université du Belvédère, Tunis), G. Boxshall (British Museum), A. Campaner, D. Defaye (Université Pierre et Marie Curie), J. Ho (California State University, Long Beach), Z. Kabata (Pacific Biological Station, Nanaimo), S. Li (Xiamen University), A. Varella (Universidade do Amazonas), and W. Vervoort kindly sent missing literature. H. Björnberg, T. Björnberg (Universidade de São Paulo), T. Bowman (Smithsonian Institution), A. Campaner, M. Dojiri

(California State University, Long Beach), M. Grygier (Smithsonian Institution), J. Ho, P. Illg (University of Washington), and J. Reid commented on drafts of the manuscript; while not agreeing with all conclusions stated here, they provided particularly helpful suggestions.

NOTES ADDED IN PROOF

In the Proceedings of the Symposium on Crustacea held in Ernakulam by the Marine Biological Association of India in 1967 Saraswathy (part 1, pp. 74-106) described copepodids I-III and the adult male of a clausidiid, *Hersiliodes laterica*; legs of the first three copepodids follow the common pattern of development. Bradford, Ohman & Jillet in *New Zealand Journal of Marine and Freshwater Research* (in press) describe six nauplii and six copepodids of calanids *Calanus australis*, *Calanoides macrocarinatus*, and *Neocalanus tonsus*. Legs 1-4 of the former two exhibit the common pattern; leg 3 of *N. tonsus* differs by attaining 3-segmented rami at CVI. Leg 5 of these three species develops like *Calanus*, described above, except for the left endopod of *Calanoides macrocarinatus* which is reduced from two to one segment at CVI. Rocha & Björnberg in *Hydrobiologia* (in press) describe all nauplii and copepodids of a cyclopid, *Alloocyrops sylvaticus*; developmental patterns of legs 1-6 are identical to those of *Apocyrops*, described above, with 2-segmented rami of legs 1-4 resulting from immediate additions after the appearance of a reorganized leg. Björnberg (1984) in her dissertation for a Masters Degree in Zoology from the Universidade de São Paulo describes nauplii and copepodids of another cyclopid, *Bryocyrops caroli*. Developmental patterns for all legs except leg 4 endopod also are similar to those of *Apocyrops*; female leg 4 endopod remains 1-segmented, while the male adds a second segment at CV. My thanks to Maria Helena Björnberg, Mark Ohman and Carlos Eduardo de Rocha for this information.

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Despite my best intentions, or pretensions, the following literature survey is not complete. I would be interested to learn from readers of *Crustaceana* about copepodid leg development in published papers, dissertations, theses, etc. describing copepod genera which I have missed in this account.

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