

Using Patterns of Appendage Development to Group Taxa of *Labidocera*, Diaptomidae and Cyclopidae (Copepoda)

Frank D. Ferrari

Smithsonian Oceanographic Sorting Center, Museum of Natural History
Smithsonian Institution, Washington, D. C. 20560, USA

Abstract

Developmental patterns for post-maxillipedal legs of copepods are used to identify (A) two monophyletic groups among 10 species of *Labidocera*, (1) *L. aestiva*, *L. rotunda* & *L. wollastoni*; and (2) *L. bengalensis*, *L. fluviatilis* & *L. pectinata*; (B) two monophyletic groups among 14 genera of Diaptomidae, (1) *Aglaodiaptomus*, *Diaptomus*, *Heliodiaptomus*, *Leptodiaptomus*, *Megadiaptomus*, *Notodiaptomus*, *Phyllodiaptomus*, *Scolodiaptomus*, & *Tumeodiaptomus*; and (2) *Allodiaptomus* & *Tropodiaptomus*; (C) three monophyletic groups among 12 genera of Cyclopidae, (1) *Acanthocyclops*, *Cyclops*, *Ectocyclops* & *Eucyclops*; (2) *Diacyclops* & *Mesocyclops*; and (3) *Allocyclops* & *Apocyclops*. To define these groups a method of weighting developmental patterns is applied which involves determining a proportion of occurrence of the pattern among all copepods and extrapolating from this proportion to an inferred possibility for the pattern's convergence within an hypothesized monophyletic lineage.

Introduction

Use of developmental patterns of copepod appendages, instead of appendage morphology of the adult alone, to infer phylogenetic relationships has been suggested recently (Ferrari 1988). Relatively complete descriptions of developmental patterns for post-maxillipedal legs have been reported for 180 taxa in five copepod orders: 56 Calanoida, 26 Cyclopoida, 53 Harpacticoida, 24 Poecilostomatoida, 21 Siphonostomatoida. Descriptions from incomplete series of copepodids add information about 5 taxa for leg 6, 16 for leg 5, 7 for leg 4, and 2 for leg 3. These descriptions provide basic information about developmental patterns of post-maxillipedal legs which is used here to compare 10 species within a calanoid genus, *Labidocera*, 14 genera within a calanoid family, Diaptomidae, and 12 genera within a cyclopoid family, Cyclopidae.

Development of copepod appendages on thoracic segments 2 through 7 (post-maxillipedal legs) usually begins in the last naupliar stage and may continue through the terminal copepodid molt (CV to CVI). Development of each leg begins as a primary bud, a thickened section of the integument armed with one or more setae. Primary

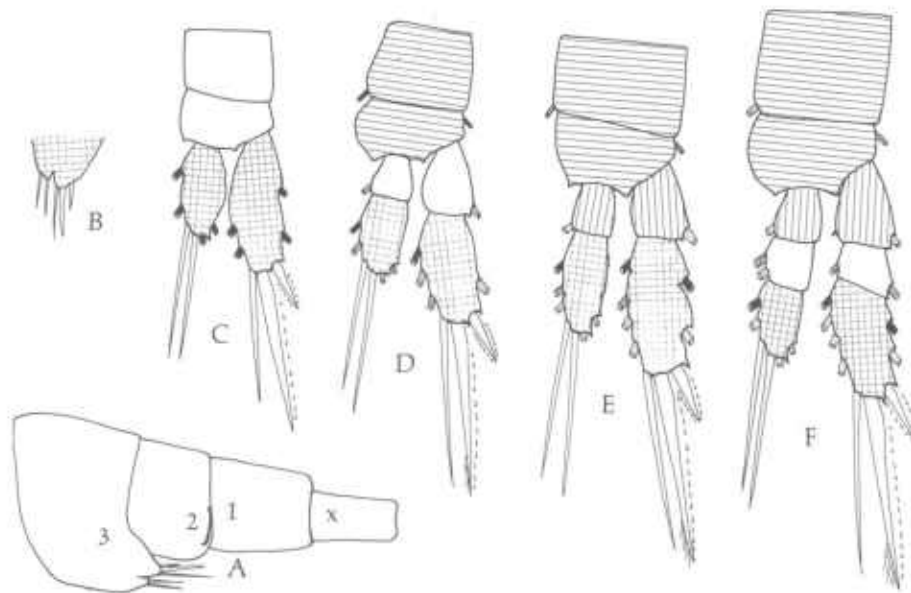


Fig. 1. Developmental stages for leg 3 of *Dioithona oculata*; A. position of primary bud on antepenultimate somite, B. primary bud, C-F. earliest to latest reorganized leg. 1=ultimate, 2=penultimate (with bud precursor), 3=antepenultimate somite; x=caudal ramus; oldest segment with cross hatching, youngest segment clear, oldest intermediate segment with horizontal hatching, youngest intermediate segment with vertical hatching; oldest setae long, youngest setae cropped and darkened, intermediate setae cropped and stippled.

Table 1. Common pattern of development for rami of copepod postmaxillipedal legs 1-4 with a general pattern of leg 5 for gymnopleans and the usual pattern of leg 6 for podopleans. N=premetamorphic nauplius; CI to CVI=first to sixth copepodid; b=primary bud; 2+2=2 exopodal plus 2 endopodal segments, etc.

	Legs					
	1	2	3	4	5	6
N	b ;	b				
CI	1+1 ;	1+1 ;	b			
CII	2+2 ;	2+2 ;	1+1 ;	b		
CIII	2+2 ;	2+2 ;	2+2 ;	1+1 ;	b	
CIV	2+2 ;	2+2 ;	2+2 ;	2+2 ;	1+1 ;	b
CV	3+3 ;	3+3 ;	3+3 ;	3+3 ;	2+2 ;	b
CVI	3+3 ;	3+3 ;	3+3 ;	3+3 ;	3+3 ;	b

buds usually appear first on the antepenultimate somite. After formation of a primary bud, a post-maxillipedal leg is reorganized to a more easily recognized copepod "swimming leg" comprising 2 basal segments, the proximal segment united to its contralateral twin by a coupler or interpodal bar, and an exopod and endopod each of one segment. Two more segments may be added to each exopod or endopod during later development (Itô 1982). Hulsemann (in press) has explained that the distalmost seg-

ment of the exopod or endopod is the oldest, the segment immediately proximal to it, if present, is the youngest, and the segment distal to the second basal segment, if present, is intermediate in age. Based on setal formation homology in leg buds of *Dioithona oculata* (Ferrari & Ambler, in preparation) this chronology can be extended to the basal segments which are regarded as intermediate in age, younger than the distalmost ramal segments but older than any other ramal segment (Fig. 1). The morphological transformations of post-maxillipedal legs during development follow a common pattern (Table 1) with several variations (Ferrari 1988).

Methods

For the taxa *Labidocera*, Diaptomidae and Cyclopidae, descriptions of post-maxillipedal legs on the last nauplius and all copepodid stages have been compiled from Gibson and Grice (1977) for *L. aestiva*, Ummerkutty (1964) for *L. bengalensis*, Li & Fang (1983) and Giesbrecht (1892) for *L. euchaeta*, Björnberg (1972) and Dahl (1894) for *L. fluviatilis*, Johnson (1935) for *L. jollae* and *L. trispinosa*, Parameswaran Pillai (1972) and Fleminger et al. (1982) for *L. pectinata*, Onbé et al. (1988) and Fleminger et al. (1982) for *L. rotunda*, and Grice & Gibson (1982) for *L. wollastoni*, Rama Devi & Ranga Reddy (1989a) for *Allodiaptomus*, Gurney (1931) for *Diaptomus*, Grandori (1913) for *Eudiaptomus* [as *Diaptomus*], Ranga Reddy & Rama Devi (1989) for *Heliodiaptomus*, Comita & Tommerdahl (1960) for *Leptodiaptomus* [as *Diaptomus*], Ranga Reddy & Rama Devi (1985) for *Megadiaptomus*, de Gouvêa (1978) for *Notodiaptomus*, Rama Devi & Ranga Reddy (1989b) for *Paradiaptomus*, Ranga Reddy & Rama Devi (1990) for *Phyllodiaptomus*, Cipólli (1973) for *Scolodiaptomus* [as *Diaptomus*], Comita & McNett (1976) for *Skistodiaptomus* [as *Diaptomus*], Rama Devi & Ranga Reddy (1990) for *Tropodiaptomus*, Varela Santibañez (1988) for *Tumeodiaptomus* [as *Diaptomus*], Lucks (1926) for *Acanthocyclops* [as *Cyclops*], Björnberg (1984) for *Bryocyclops*, Gurney (1932) for *Cyclops*, Auvray & Dussart (1966) for *Eucyclops*, Defaye (1984) for *Macrocylops*, and de Gouvêa (1978) and Silva et al. (1989) for *Thermocyclops*.

Descriptions of copepodid appendages alone have been taken from Taw (1974) for *L. tasmanica*, Kamal and Armitage (1967) for *Aglaodiaptomus* [as *Diaptomus*], Valderhaug & Kewalramani (1979) for *Apocyclops*, Amores-Serrano (1978) for *Diacyclops* and *Mesocyclops* [both as *Cyclops*], Candeias (1966) for *Halicyclops*, and Carvalho (1971) for *Ectocyclops*. In addition unpublished descriptions of nauplii and copepodids of *Alloicyclops* were provided by Rocha & Björnberg (in preparation).

A database file has been established with numbers of basipodal and ramal segments of post-maxillipedal legs for each copepodid and the last nauplius for each different specific plan of development reported for a genus. If more than one plan has been reported for the same species, each is entered. Further information about this database file is available from the author. The assumption which underlies the operational rules of this study is that transformations of segment numbers which are observed during copepod development are similar in kind and frequency to those that have occurred during copepod evolution.

Table 2. Developmental pattern of legs 1-4 and female leg 5 for all species of *Labidocera*. Abbreviations as in Table 1.

	Legs				
	1	2	3	4	5
N	b ;	b			
CI	1+1 ;	1+1 ;	b		
CII	2+1 ;	2+1 ;	1+1 ;	b	
CIII	2+1 ;	2+1 ;	2+1 ;	1+1 ;	b
CIV	2+1 ;	2+1 ;	2+1 ;	2+1 ;	1+1
CV	3+2 ;	3+2 ;	3+2 ;	3+2 ;	1+1
CVI	3+2 ;	3+2 ;	3+2 ;	3+2 ;	1+1

Table 3. Developmental patterns for male leg 5 among species of *Labidocera*; *trispinosa* has a 1-segmented endopod on its left leg (indicated in parentheses). Species are listed below pattern; lower data indicate number of taxa among copepod orders in which the pattern also is found; cal=Calanoida, cyc=Cyclopoida, har=Harpacticoida, pec=Poecilostomatoida, sif=Siphonostomatoida; other abbreviations as in Table 1.

	A	B	C	D	E	F
CIV	1+0	1+1	1+1	1+1	1+1	2+1
CV	1+0	1+0	1+1	1+1	2+1	2+1
CVI	2+0	2+0	2+0	2+0	2+0	2+(1)0
	<i>aestiva</i>	<i>bengalensis</i>	<i>tasmanica</i>	<i>euchaeta</i>	<i>jollae</i>	<i>trispinosa</i>
	<i>rotunda</i>	<i>fluviatilis</i>				
	<i>wollastoni</i>	<i>pectinata</i>				
61 cal	5/61		1/61			
26 cyc						
56 har						
24 pec						
21 sif						

Results

Legs 1-4 of mature females and males, and leg 5 of mature females in the 10 species of *Labidocera* listed above have the same number of exopod and endopod segments, and the developmental pattern for each leg is identical among all species (Table 2). Ramal segment numbers for leg 5 of adult males are identical (2-segmented exopod, endopod absent) except for *L. trispinosa* whose left leg 5 has a 1-segmented endopod. However, among males there are six developmental patterns for leg 5; four occur in one species only (Table 3). Among these, the pattern for *L. tasmanica* occurs in only one other copepod genus, males of the calanoid *Heterocope*. The pattern shared by *L. fluviatilis*, *L. bengalensis* and *L. pectinata* is unique among copepod taxa. The pattern shared by *L. aestiva*, *L. rotunda* and *L. wollastoni* also has been reported for males of *Calanopia*, *Paralabidocera*, *Pontella*, *Temora*, and females of *Eurytemora*.

Table 4. Developmental patterns for leg 1 among diaptomid genera. aglao=*Agladiaptomus*, eu=*Eudiaptomus*, noto=*Notodiaptomus*, tumeo=*Tumeodiaptomus*; * genera are *Allodiaptomus*, *Diaptomus*, *Heliodiaptomus*, *Leptodiaptomus*, *Megadiaptomus*, *Paradiaptomus*, *Phyllodiaptomus*, *Scolodiaptomus*, *Skistodiaptomus*, and *Tropodiaptomus*; abbreviations as in Table 1.

	A	B	C	D	E
CI	1+1	1+1	1+1	2+2	1+1
CII	2+2	2+1	1+1	2+2	2+1
CIII	2+2	2+1	2+1	2+2	2+2
CIV	2+2	2+2	2+2	2+2	2+2
CV	3+2	3+2	3+2	3+2	3+3
CVI	3+2	3+2	3+2	3+2	3+2
	10 diaptomids*	eu	aglao	tumeo	noto
42 cal	10/42				
26 cyc	13/26				
53 har	23/53				
24 pec	9/24				
21 sif					

Table 5. Developmental patterns for leg 2 among diaptomid genera. eu=*Eudiaptomus*, para=*Paradiaptomus*, tumeo=*Tumeodiaptomus*; * genera are *Agladiaptomus*, *Allodiaptomus*, *Diaptomus*, *Heliodiaptomus*, *Leptodiaptomus*, *Megadiaptomus*, *Notodiaptomus*, *Phyllodiaptomus*, *Scolodiaptomus*, *Skistodiaptomus*, and *Tropodiaptomus*; see Fig. 4 for other abbreviations.

	A	B	C	D
CI	1+1	1+1	2+2	2+2
CII	2+2	1+1	2+2	2+2
CIII	2+2	1+1	2+2	2+2
CIV	2+2	2+2	2+2	2+2
CV	3+3	3+3	3+3	3+3
CVI	3+3	3+3	3+3	3+3
	11 diaptomids*	eu	para	tumeo
42 cal	8/42	1/42		
26 cyc	12/26			
53 har	26/53			
24 pec	11/24			
21 sif				

Adults of all diaptomid genera reported above have 3-segmented rami on legs 1-4 except the 2-segmented endopod of leg 1. Among genera, each leg exhibits some variability in developmental pattern. One pattern for each leg is shared among 10-13 genera, and also is represented among many other copepod taxa. Each variation from that pattern for each leg is found in a single diaptomid genus (Tables 4-7). Leg 5 varies in both final segment number and developmental pattern (Table 8). Its variation is expressed among genera, between females and males of the same genus, and within left and right male leg 5. Five developmental patterns are found in only one

Table 6. Developmental patterns for leg 3 among diaptomid genera. aglao=*Aglaodiaptomus*, eu=*Eudiaptomus*, tumeo=*Tumeodiaptomus*; * genera are *Allodiaptomus*, *Diaptomus*, *Heliodiaptomus*, *Leptodiaptomus*, *Megadiaptomus*, *Notodiaptomus*, *Paradiaptomus*, *Phyllodiaptomus*, *Scolodiaptomus*, *Skistodiaptomus*, and *Tropodiaptomus*; see Fig. 4 for other abbreviations.

	A	B	C	D
CII	1+1	1+1	1+1	2+2
CIII	2+2	2+2	2+1	2+2
CIV	2+2	3+2	2+2	3+3
CV	3+3	3+3	3+3	3+3
CVI	3+3	3+3	3+3	3+3
	11 diaptomids*	aglao	eu	tumeo
44 cal	15/44		1/44	
26 cyc	11/26			
53 har	28/53			
24 pec	12/24			
21 sif				

Table 7. Developmental patterns for leg 4 among diaptomid genera. tumeo=*Tumeodiaptomus*; * genera are *Aglaodiaptomus*, *Allodiaptomus*, *Diaptomus*, *Eudiaptomus*, *Heliodiaptomus*, *Leptodiaptomus*, *Megadiaptomus*, *Notodiaptomus*, *Paradiaptomus*, *Phyllodiaptomus*, *Scolodiaptomus*, *Skistodiaptomus*, and *Tropodiaptomus*; see Fig. 4 for other abbreviations.

	A	B
CIII	1+1	2+2
CIV	2+2	3+3
CV	3+3	3+3
CVI	3+3	3+3
	13 diaptomids*	tumeo
46 cal	17/46	
26 cyc	13/26	1/26
55 har	27/55	1/55
24 pec	7/24	
21 sif		

genus and four in two or more. In nine genera (*Allodiaptomus*, *Eudiaptomus*, *Megadiaptomus*, *Notodiaptomus*, *Paradiaptomus*, *Phyllodiaptomus*, *Scolodiaptomus*, *Tropodiaptomus*, and *Tumeodiaptomus*) patterns differ between females and males, and in two of those (*Allodiaptomus*, and *Tropodiaptomus*) patterns differ within left and right male legs.

Cyclopoid genera exhibit variation for legs 1-5 in final segment number and in developmental patterns (Tables 9-13). Thirteen of 25 patterns are limited to a single genus. In three genera patterns differ between females and males—*Macrocylops* for leg 3, *Bryocyclops* for leg 4 and *Apocyclops* for leg 5; asymmetrical developmental patterns are absent.

Table 8. Developmental patterns for leg 5 among diaptomid genera. f=female, ml=male left leg, mr=male right leg; aglao=*Agladiaptomus*, allo=*Allodiaptomus*, diap=*Diaptomus*, eu=*Eudiaptomus*, helio=*Heliodiaptomus*, lepto=*Leptodiaptomus*, mega=*Megadiaptomus*, noto=*Notodiaptomus*, para=*Paradiaptomus*, phylo=*Phylodiaptomus*, sco=*Scolodiaptomus*, sks=*Skistodiaptomus*, tropo=*Tropodiaptomus*, tumeo=*Tumeodiaptomus*; see Fig. 4 for other abbreviations.

	A	B	C	D	E	F	G	H	I
CIV	1+1	1+1	1+1	1+1	1+1	1+1	1+1	1+1	1+1
CV	2+1	2+1	2+1	2+1	1+0	2+1	2+2	2+2	2+0
CVI	2+1	1+1	3+1	3+2	2+2	2+2	2+2	3+2	2+1
	aglao	allo ml	allo f	tumeo f	eu m	para f	para m	phylo f	sks
	allo mr	tropo ml	mega f	eu f					
	diap		noto f						
	helio		sco f						
	lepto		tropo f						
	mega m								
	noto m								
	phylo m								
	sco m								
	tropo mr								
	tumeo m								

53 cal 1/53
cyc, har, pec, sif=none

Discussion

Among *Labidocera*, Diaptomidae and Cyclopidae, 33 leg developmental patterns are found in only one taxon. Of these patterns, 24 are not found among the remaining copepod taxa, nine are found in less than 5% of the remaining taxa and one in more than 5%. These developmental patterns are useful in differentiating their single representative taxon from related taxa.

In contrast there are 23 developmental patterns with more than one representative within *Labidocera*, Diaptomidae and Cyclopidae. These patterns can be used to define multitaxa groups descended from a common ancestor. For example the developmental pattern for leg 5 of *L. bengalensis*, *L. fluviatilis* and *L. pectinatus* (Table 3B) is not found in any other copepod. The most likely hypothesis is that these three species are derived from a common ancestor with that pattern and therefore grouping these taxa based on that pattern is preferred here.

In defining multi-taxa groups, a problem arises when a taxon can be placed in more than one multi-taxa group. This problem may result when a taxon expresses different developmental patterns in: left and right members of the same leg (asymmetrical dimorphism in leg 5 of diaptomids); the same leg for male and female (sexual dimorphism in leg 5 of diaptomids and legs 3-5 of cyclopids); different legs.

A solution used here is to assign different weights to different developmental patterns; if the result is equivocal then different weights are assigned to the kinds of

transformations that comprise a developmental pattern. The operation and logic of weighting are as follows: (1) determine the proportion of occurrence among all remaining taxa of a specific developmental pattern or an individual transformation; (2) extrapolate from the proportion of occurrence to an inferred possibility for convergence for that character such that a higher proportion of occurrence among remaining taxa suggests a higher inferred possibility for convergence [the following is implicit—as the proportion of occurrence increases, the probability that at least in one case the pattern is due to convergence also increases]; (3) conclude that a higher inferred possibility for convergence of that pattern increases the likelihood that a multi-species group defined by the pattern is polyphyletic.

For example the developmental pattern for leg 2 of 11 diaptomids (Table 5A) also is reported in 57 of 166 other copepod taxa (about one-third). The high proportion of occurrence of this pattern may result from its retention as the ancestral pattern, or it may result from one or more convergences to that pattern from dissimilar ancestors. That is, this pattern has originated independently among several taxa within the copepods and has been selected positively each time it originated. Based on such a developmental pattern with a high proportion of occurrence, a group will be presumed to be monophyletic only if there are no other data to the contrary from patterns with low proportions of occurrence.

Sexual or asymmetrical dimorphism in leg development results in a taxon with several developmental patterns for the same leg. Among diaptomids and cyclopids, a taxon expressing such variation may be placed in more than one multi-taxa group. Proportion of occurrence data may indicate which pattern is more likely to have resulted from convergence and this repetitive pattern would have a less likely monophyletic certainty. In addition, three simple empirically derived operational rules about occurrences of developmental transformations, which are the individual steps of a developmental pattern, provide further information to resolve such dilemmas. For copepod development in general (Ferrari 1988), (1) developmental transformations in which a segment number is reduced from a higher number earlier in development are rare; (2) transformations which are accelerated [occurring earlier in development than expected, using the common pattern as a reference] are rarer than transformations which are delayed [occurring later in development than expected, based on the common pattern]; (3) delayed transformations of the exopod and endopod together are rarer than delayed transformations of the endopod alone. It is reasonable to extrapolate from these relative proportions of occurrence through inferred possibilities for convergence to presumed monophyletic groups. If a taxon can be placed in more than one multitaxa group based on differences among leg developmental patterns and proportions of occurrence for those patterns do not favor one pattern over the others, then the kinds of transformations comprising the developmental patterns will be evaluated in this order of preference [highest to lowest]: reductions, accelerations, delay exopod and endopod, delay endopod only.

Development of leg 5 provides the only information for grouping *Labidocera* (Table 3). There are six patterns for leg 5 development. Two multi-taxa groups are (1) *L. aestiva*, *L. rotunda*, and *L. wollastoni*; (2) *L. bengalensis*, *L. fluviatilis*, *L. pectinata*. In

pattern A (Table 3), which defines group (1) three of the five other calanoids having this pattern are pontellid genera, confamilial with *Labidocera*; pattern B, which defines group (2), is not shared with any other copepod. The second group has a lower inferred possibility for convergence of characters and a higher monophyletic certainty than the first.

Previous studies of *Labidocera* (Fleminger 1967, Fleminger et al. 1982) have utilized adult sexually modified characters and geographic distributions to place some species into species groups and those into complexes (more than one species group); the status of many species still is unresolved. Species in group (1), as defined in the present study, are found in neritic zones of the Indo-Pacific (*L. rotunda*), and eastern (*L. wollastoni*) and western (*L. aestiva*) North Atlantic; all presumably would belong to different species groups in different complexes. Among species of group (2), as defined in the present study, two (*L. bengalensis* and *L. pectinata*) belong to different species groups in the same Indo-Pacific complex, while the third (*L. fluviatilis*), from the western North Atlantic, presumably belongs to a different complex. Phylogenetic hypotheses which successfully incorporate data from the present and previous studies will require splitting the ancestral species of *Labidocera* at least once prior to episodes which are responsible for the present distribution of complexes of species groups confined to neritic zones of the Indo-Pacific, and eastern and western North Atlantic Oceans.

Development of legs 1-5 provides information for grouping diaptomid genera. However, information for legs 1-4 is not preferred because of the high proportion of occurrence for the multi-taxa group of each leg. There are nine patterns of development for leg 5 (Table 8). Proportion of occurrence among other copepod taxa is low for all patterns and so an inferred possibility for convergence is low for each. Some

Table 9. Developmental patterns for leg 1 among cyclopid genera. allo=*Allocyclops*, apo=*Apocyclops*, bryo=*Bryocyclops*, dia=*Diacyclops*, meso=*Mesocyclops*, thermo=*Thermocyclops*; *=*Acanthocyclops*, *Cyclops*, *Ectocyclops*, *Eucyclops*, *Halicyclops*, *Macrocyclus*; see Fig. 4 for other abbreviations.

	A	B	C	D
CI	1+1	1+1	1+1	1+1
CII	2+2	2+2	2+2	2+2
CIII	2+2	2+2	2+2	2+2
CIV	2+2	2+2	2+2	2+2
CV	3+3	2+2	2+2	2+3
CVI	3+3	3+3	2+2	3+3
	6 cycloids*	meso dia	allo apo bryo	thermo
56 cal	10/56			
14 cyc	7/14			
53 har	23/53		2/53	
24 pec	9/24	3/24	1/24	
21 sif			1/21	

Table 10. Developmental patterns for leg 2 among cyclopid genera. allo=*Allocyclops*, apo=*Apocyclops*, bryo=*Bryocyclops*, hali=*Halicyclops*, meso=*Mesocyclops*, thermo=*Thermocyclops*; *=*Acanthocyclops*, *Cyclops*, *Diacyclops*, *Ectocyclops*, *Eucyclops*, *Macrocylops*; see Fig. 4 for other abbreviations.

	A	B	C	D	E
CI	1+1	1+1	1+1	1+1	1+1
CII	2+2	2+2	2+2	1+1	2+2
CIII	2+2	2+2	2+2	2+2	2+2
CIV	2+2	2+2	2+2	2+2	2+3
CV	3+3	2+2	2+2	3+3	3+3
CVI	3+3	3+3	2+2	3+3	3+3
	6 cycloids*	meso	allo apo bryo	hali	thermo
56 cal	8/56				
14 cyc	6/14				
53 har	26/53				
24 pec	11/24	3/24			
21 sif			1/21	1/21	

Table 11. Developmental patterns for leg 3 among cyclopid genera. allo=*Allocyclops*, apo=*Apocyclops*, bryo=*Bryocyclops*, macro=*Macrocylops*, meso=*Mesocyclops*, thermo=*Thermocyclops*; *=*Acanthocyclops*, *Cyclops*, *Diacyclops*, *Ectocyclops*, *Eucyclops*, *Halicyclops*; see Fig. 8 for other abbreviations.

	A	B	C	D	E
CII	1+1	1+1	1+1	1+1	1+2
CIII	2+2	2+2	2+2	2+2	2+2
CIV	2+2	2+2	2+2	3+3	2+3
CV	3+3	2+2	2+2	3+3	3+3
CVI	3+3	3+3	2+2	3+3	3+3
	6 cycloids* macro f	meso	allo apo bryo	macro m	thermo
58 cal	15/58	1/58			
14 cyc	5/14				
53 har	28/53			1/53	
24 pec	12/24	3/24			
21 sif					

genera express sexual dimorphism or male asymmetrical dimorphism, and can be assigned to more than one multi-taxa group. Using developmental transformation rules, *Allodiaptomus*, and *Tropodiaptomus* are placed in a group defined by pattern B with an exopodal segment reduction from CV to CVI rather than in patterns A or C which involve delayed transformations only. *Megadiaptomus*, *Notodiaptomus*, and *Scolodiaptomus* are placed in a group defined by pattern A with delayed transformations of exopod and endopod together rather than in pattern C with delayed transfor-

Table 12. Developmental patterns for leg 4 among cyclopid genera. allo=*Allocyclops*, apo=*Apocyclops*, bryo=*Bryocyclops*, meso=*Mesocyclops*, thermo=*Thermocyclops*; *=*Acanthocyclops*, *Cyclops*, *Diacyclops*, *Ectocyclops*, *Eucyclops*, *Halicyclops*, *Macrocylops*; see Fig. 8 for other abbreviations.

	A	B	C	D	E
CIII	1+1	1+1	1+1	1+1	1+1
CIV	2+2	2+2	2+2	2+1	2+1
CV	3+3	2+2	2+2	2+1	2+2
CVI	3+3	3+3	2+2	2+1	2+2
	7 cyclopid*	meso	allo	bryo f	bryo m
		thermo	apo		
60 cal	17/60				
14 cyc	6/14				
55 har	27/55				
24 pec	7/24				
21 sif					

Table 13. Developmental patterns for leg 5 among cyclopid genera. b=bud, 1=1 basal segment, 1/1=1 basal & 1 exopodal segment; acanth=*Acanthocyclops*, allo=*Allocyclops*, apo=*Apocyclops*, bryo=*Bryocyclops*, cyc=*Cyclops*, dia=*Diacyclops*, ecto=*Ectocyclops*, eu=*Eucyclops*, hali=*Halicyclops*, macro=*Macrocylops*, meso=*Mesocyclops*, thermo=*Thermocyclops*; see Fig. 8 for other abbreviations.

	A	B	C	D	E	F
CIII	b	b	b	b	b	1/1
CIV	b	b	b	b	1/1	1/1
CV	b	b	1	1/1	1/1	1/1
CVI	b	1	1	1/1	1/1	1/1
	allo	apo f	thermo	eu	acantho	macro
	apo m				cyc	
	bryo				dia	
	ecto				hali	
					meso	
67 cal					2/67	
14 cyc	3/14	1/14	3/14			
56 har	10/56	15/56	7/56	7/56	13/56	
24 pec	6/24	1/24	1/24			
21 sif	14/21					

mations of the endopod alone. *Phylloidiaptomus* and *Tumeodiaptomus* also are placed in a group defined by pattern A rather than ones defined by patterns D or H with a delayed transformation of an endopod alone. Thus there are two multi-taxa groups (1) *Aglaodiaptomus*, *Diaptomus*, *Heliodiaptomus*, *Leptodiaptomus*, *Megadiaptomus*, *Notodiaptomus*, *Phylloidiaptomus*, *Scolodiaptomus*, and *Tumeodiaptomus* and (2) *Allodiaptomus* and *Tropodiaptomus*. Both groups have a low inferred possibility for con-

vergence of characters and thus a high monophyletic certainty.

Among cyclopid genera there are several developmental patterns for each leg and several multi-taxa groups can be formed (Tables 9-13). The following groups are preferred (1) *Acanthocyclops*, *Cyclops*, *Ectocyclops*, and *Eucyclops*. This group shares similar developmental patterns for legs 1-4. The proportion of occurrence for those patterns among copepod genera is high; the inferred possibility for convergence also is high. Because there are no other data to the contrary, this multi-taxa group is accepted. (2) *Diacyclops* and *Mesocyclops*; these share delayed transformations of exopod and endopod segments of leg 1 and an identical developmental pattern of leg 5. *Thermocyclops* and *Mesocyclops* share delayed transformations of exopod and endopod segments of leg 4 but differ in their developmental patterns of leg 5. (3) *Allocyclops* and *Apocyclops*; these share delayed transformations of exopod and endopod of legs 1-4. *Halicyclops* is removed from group (1) because it alone expresses delayed transformation of an exopod and endopod of leg 3 (Table 11). *Macrocylops* is removed from group (1) because it alone expresses accelerated transformation of an exopod and endopod of leg 3 (Table 11). *Bryocyclops* is removed from group (3) because it alone expresses delayed transformation of an endopod of leg 4 (Table 12).

Kiefer (1928) provided an exhaustive system of classification for the Cyclopidae. The basis for the groupings was number and position of setae on the articulating segment of leg 5 of adults. Although many of Kiefer's subgenera now are recognized as genera and new genera have been added, the foundation of his system is accepted today. It is clear that the groups of cyclopid genera presented here cannot be integrated into Kiefer's system. Specifically the exclusions of *Macrocylops* from group (1) and *Thermocyclops* from group (2) are incompatible with Kiefer's system.

In conclusion developmental patterns of post-maxillipedal legs provide information for purposes of differentiating and grouping taxa among *Labidocera*, Diaptomidae and Cyclopidae. Empirically derived constructs such as proportion of occurrence of patterns or of developmental transformations can be extrapolated to estimate the likelihood of character convergence, and so can resolve dilemmas which arise when the same taxon may be placed in more than one multi-taxa group.

Acknowledgments

Tagea K. S. Björnberg and her many students deserve special thanks for their continued interest in studies of copepod development. Thomas E. Bowman, Jon Norenburg, and Janet Reid of the Smithsonian Institution reviewed the manuscript and provided many valuable suggestions; however, their participation does not imply agreement with the conclusions offered here.

Literature Cited

- Amores-Serrano, R., 1978. Life histories and seasonal population dynamics of two cyclopid copepods in Beaver Reservoir, Arkansas, including some observations on their post-embryonic development. *Thesis and Dissertation Series*, no. 17, Univ. Arkansas, 89pp.
- Auvray, C. & B. Dussart, 1966. Rôle de quelques facteurs du milieu sur le développement post-embryonnaire des Cyclopidés (Crustacés Copepodes). I.—Généralités. *Cas de Eucyclops*. *Bull. Soc. Zool. France* 91:

- 477-491.
- Björnberg, M., 1984. Descrição de *Bryocyclops caroli* sp. n. estudo comparativo do desenvolvimento pos-embrionário de *B. caroli* e *B. absalomi* Por, 1981 (Copepoda, Cyclopoida, Cyclopidae). *Dissertacao, Mestre em Zoologia, Univ. Sao Paulo*, 75pp.
- Björnberg, T., 1972. Developmental stages of some tropical and subtropical planktonic marine copepods. *Studies Fauna Curacao Carib. Islands*, 40:1-185.
- Candeias, A., 1966. Contribution to the knowledge of the development of *Halicyclops neglectus* Kiefer. *Rev. Biol. Lisbon*, 4:171-186.
- Carvalho, M., 1971. Desenvolvimento de *Ectocyclops rubescens* (Brady 1904) (Copepoda, Crustacea). *Bolm. Fac. Filos. Cienc. Univ. S. Paulo, Zool. Biol. Mar.*, (n. ser.) 28:343-388.
- Cipólli, M., 1975. Morfologia externa das fases de desenvolvimento de *Diaptomus corderoi* Wright, 1936 (Crustacea, Copepod, Calanoida). *Bolm. Fac. Filos. Cienc. Univ. S. Paulo, Zool. Biol. Mar.*, (n. ser.) 30:567-612.
- Comita, G. & D. Tommerdahl, 1960. The postembryonic developmental instars of *Diaptomus siciloides* Lilljeborg. *J. Morphology*, 107:297-356.
- Comita, G. & S. McNett, 1976. The postembryonic developmental instars of *Diaptomus oregonensis* Lilljeborg, 1889 (Copepoda). *Crustaceana*, 30:123-163.
- Dahl, F., 1894. Die Copepodenfauna des unteren Amazonas. *Ber. Naturforsch. Ges. Freiburg i. B.*, 8:10-23.
- Defaye, D., 1984. Développement et nutrition chez *Macrocyclus albidus* (Crustacé, Copépe). *Thèse Doctorate Biologie et Physiologie animales, Univ. Bordeaux I*, 1-107+19 plts.
- de Gouvêa, E., 1978. Estégios de desenvolvimento pós embrionário de *Thermocyclops minutus* (Lowndes) e de *Notodiaptomus conifera* (Sars) (Crustacea, Copepoda) da Lagoa do Abaeté (Salvador—Ba.). *Tese Doutor em Ciências, Univ. Sao Paulo*, 131pp.
- Ferrari, F., 1988. Developmental patterns in numbers of ramal segments of copepod post-maxillipedal legs. *Crustaceana*, 54:256-293.
- Ferrari, F., & J. Ambler, [in preparation]. Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Oithonidae).
- Fleminger, A., 1967. Taxonomy, distribution and polymorphism in the *L. jollae* group with remarks on evolution within the group (Copepoda: Calanoida). *Proc. U. S. Nat. Mus.*, 120:1-61.
- Fleminger, A., B. Othman, & J. Greenwood, 1982. The *Labidocera pectinata* group: an Indo-West Pacific lineage of planktonic copepods with descriptions of two new species. *J. Plankton Res.*, 4:245-270.
- Gibson, V. & G. Grice, 1977. The developmental stages of *Labidocera aestiva* Wheeler, 1900 (Copepoda, Calanoida). *Crustaceana*, 32:7-20.
- Giesbrecht, W., 1892. Systematik und Faunistic der Pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna Flora Golf. Neapel*, 19:1-831, 54plts.
- Grandori, R., 1913. Studi sullo sviluppo larvale dei copepodi pelagici. *Redia*, 8:360-457.
- Grice, G. & V. Gibson, 1982. The developmental stages of the calanoid copepod *Labidocera wollastoni* (Lubbock) with observations on its eggs. *Cah. Biol. Mar.*, 23:215-225.
- Gurney, R., 1931. *British Freshwater Copepoda*. 1. 228pp. The Ray Society, London.
- Gurney, R., 1932. *British Freshwater Copepoda*. 2. 336pp. The Ray Society, London.
- Hulsemann, K., (in press). The copepodid stages of *Drepanopus forcipatus* Giesbrecht, with notes on the genus and a comparison to other members of the family Clausocalanidae (Copepoda Calanoida). *Helgolander Meeresunters.*
- Itô, T., 1982. The origin of 'biramous' copepod legs. *J. nat. Hist.*, 16:715-726.
- Johnson, M., 1935. The developmental stages of *Labidocera*. *Biol. Bull. mar. biol. Lab. Woods Hole*, 68:397-421.
- Kamal, A. & K. Armitage, 1967. External morphology of adult and copepodid stages of *Diaptomus clavipes* Schacht 1897. *Univ. Kansas Sci. Bull.*, 47:559-573.
- Kiefer, F., 1928. Ueber Morphologie und Systematik der Süßwasser-Cyclopiden. *Zool. J., Syst.*, 54:495-556.
- Li, S. & J. Fang, 1983. The developmental stages of *Labidocera euchaeta* Giesbrecht. *J. Xiamen Univ. (Nat. Sci.)*, 22:96-101. [in Chinese]

- Lucks, R., 1926. Zur Entwicklungsgeschichte des *Cyclops viridis* Jurine und seiner Stellung zum *Cyclops clausii* Heller. *Schr. Naturf. Ges. Danzig*, 17:128-169.
- Onbé, T., T. Hotta, & S. Ohtsuka, 1988. The developmental stages of the marine calanoid copepod *Labidocera rotunda*. *J. Fac. appl. biol. sci., Hiroshima Univ.*, 27:79-91.
- Parameswaran Pillai, P., 1971. On the post-naupliar development of the calanoid copepod *Labidocera pectinata* Thompson and Scott (1903). *J. mar. biol. Ass. India*, 13:66-77.
- Rama Devi, C. & Y. Ranga Reddy, 1989a. The complete postembryonic development of *Allodiptomus raoi* Kiefer, 1936 (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, 56:246-266.
- Rama Devi, C. & Y. Ranga Reddy, 1989b. The complete postembryonic development of *Paradiaptomus greeni* (Gurney, 1906) (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, 56:141-161.
- Rama Devi, C. & Y. Ranga Reddy, 1990. The complete postembryonic development of *Tropodiptomus informis* Kiefer, 1936 (Copepoda: Calanoida) reared in the laboratory. *J. Plankton Res.*, 12:55-75.
- Ranga Reddy, Y. & C. Rama Devi, 1985. The complete postembryonic development of *Megadiptomus hebes* Kiefer, 1936 (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, 48:40-63.
- Ranga Reddy, Y. & C. Rama Devi, 1989. The complete postembryonic development of *Heliodiptomus contortus* (Gurney, 1907) (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, 57:113-133.
- Ranga Reddy, Y. & C. Rama Devi, 1990. Postembryonic development of *Phyllodiptomus blanci* (Guerne & Richard, 1896) (Copepoda, Calanoida). *Hydrobiologia*, 190:155-170.
- Rocha, C. & M. Bjornberg, [in preparation]. Description and developmental stages of a new *Allocyclops* species from Brazil.
- Silva, E., B. Robertson, J. Reid, & E. Hardy, 1989. Atlas de copépodos planctônicos, Calanoida e Cyclopoida (Crustacea), da Amazônia Brasileira. I. *Represa Curuá-Una, Pará. Rev. Brasileira Zool.*, 6: 725-758.
- Taw, N., 1974. A new species of *Labidocera*. (Copepoda: Calanoida) from Tasmania and its postnaupliar developmental stages. *Aust. J. mar. freshw. Res.*, 25:261-272.
- Ummerkutty, A., 1964. Studies on Indian copepods 6. The postembryonic development of two calanoid copepods, *Pseudodiptomus auriwilli* Cleve and *Labidocera bengalensis* Krishnaswamy. *J. mar. biol. Ass. India*, 6:48-60.
- Valderhaug, V. & H. Kewalramani, 1979. Larval development of *Apocyclops dengizicus* Lepeshkin (Copepoda). *Crustaceana*, 36:1-8.
- Varela Santibañez, C., 1988. Desarrollo post-embrionario de *Diptomus diabolicus* Brehm (Copepoda, Calanoida) del sur de Chile. *Biota de Osorno, Chile*, 4:31-61.